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New Acrotretid Brachiopods from North and South America and an Examination of their Functional Morphology

By

Jennifer Anne Duffy ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science.

Department of Earth and Atmospheric Sciences

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ABSTRACT

Acrotretid brachiopods are described for the first time from the Ordovician of northern Argentina. Four Ordovician (Arenig and Llanvirn) localities in the Argentine Precordillera yielded eight new species as well as one species previously described from Sweden. New species are also described from the Silurian of Oklahoma and the Canadian arctic, doubling the North American species diversity of the acrotretids for this time period. Three new species are from the Lower Silurian (Wenlock) of Cornwallis Island and one is from the Wenlock of the Northwest Territories. Two previously described species are identified from the Silurian of Oklahoma.

Based solely on the morphological features of both the larval and adult shell, the habitat of highly conical acrotretids is interpreted to have been planktonic. An extensive examination of the larval pits is provided and three general pitting arrangements are suggested. Two morphological groups are proposed: the 'benthic' group, is characterized by the densely built, compact shell of *Artiotreta* Ireland; and the 'epiplanktonic' group, which is characterized by the highly conical lightly built shell of *Opsiconidion* Ludvigsen.

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CHAPTER 1

Introduction and General Characteristics of the Acrotretids

INTRODUCTION

The acrotretids are a group of small (less than 2 mm in width) inarticulated brachiopods that extend from the Cambrian to the Devonian and have been described from localities representing various paleoenvironments on every continent but Africa. The wide geographical and environmental distribution, coupled with various morphological features, has spurred a debate surrounding what habitat these small brachiopods may have occupied. They are considered to be important paleoenvironmental indicators during the Cambrian and Ordovician, but are relatively scarce in the Silurian and Devonian deposits of the world.

The importance of the present work is threefold: 1) it represents the first acrotretids described from the Ordovician of Argentina, 2) the description of new species from the Silurian of North America serves to double the diversity of the acrotretids during the Silurian, and 3) it is the first morphological examination of the life mode for highly conical acrotretids, shedding new light on the issue of their habitat. In addition, a general introduction to the acrotretids is provided below.

Terminology

The pitted larval valve will be referred to as the 'larval' or 'first formed' valve, and not the 'protegulum', following Rowell (1989, p. 1056), who pointed out that this term should only be applied to a shell secreted by an embryo while still within an egg.

The valve bearing the foramen will be referred to, interchangeably, as the pedicle or ventral valve. Likewise, the valve opposite the pedicle valve will be referred to as the brachial or dorsal valve. Other terms are used in accordance with the morphological and anatomical terms as provided in the Treatise on Invertebrate Paleontology H (Williams and Brunton, 1997).

Techniques

Samples were processed through acid preparation using the acetic buffering technique (Jeppsson et al., 1985: 952-by "mixing 7% concentrated acetic acid, 63% water, and 30% of the solution left after the dissolution of previous samples") for fossils of calcium phosphate. Once the matrix had broken down sufficiently, the sample was washed through four successively finer sieves, and then dried until it was ready to be picked under a dissecting microscope. Appropriate specimens were mounted for the Scanning Electron Microscope, on developed film, using a water-soluble gum tragacanth, and sputter coated with gold for increased conductivity (to prevent charging during imaging). All images are Scanning Electron Micrographs.

Repository

All specimen numbers with the prefix UA (13179-13218) are housed in the Type Collections at the Department of Earth and Atmospheric Sciences, University of Alberta, Edmonton, T6G 2E3, Canada. Those with the prefix CEGH-UNC (19851-19631) are housed at the Catedra de Estratigraphia y Geologia Historica, Universidad Nacional de Cordoba, Avenida Velez Sarsfield 299, 5000 Cordoba, Argentina.

General Introduction to Acrotretid Brachiopods

Phylum Brachiopoda

Brachiopods are a group of solitary metazoans that possess a mineralized bivalved shell that is bilaterally symmetrical about the median plane. They are sedentary animals that usually attach to substrata with a fleshy stalk called a pedicle and filter feed through the means of a ciliated lophophore. The group can be allied with phoronids and bryozoans based on the presence of this lophophore. Brachiopods are exclusively marine and generally occupy the shallow continental shelf; however, some representatives may have occupied marginal marine environments with a variable salinity tolerance of 17-45%, and they have been found at depths of 6000 m. There are approximately 3200 named genera within the phylum, which has existed from the Early Cambrian and is represented by 100 living genera.

Traditionally, the phylum has been split into two groups based mainly on the presence or absence of a skeletal articulation at the posterior shell interface, with Class Articulata comprised of forms possessing a tooth and socket joint holding the two valves together at a hinge, while members of Class Inarticulata did not possess this hard part articulation and their valves were held together solely by muscles (i.e. Moore, 1965). Recently, however, there has been much discussion on brachiopod classification (Williams *et al.*, 1996). The most recent scheme includes three subphyla, which are distinguished based mainly on their mineral composition and this condition of the posterior part of the shell. Subphylum Rhynchonelliformea is made up of those forms that were formerly classified within Class Articulata. They are characterized by a calcium carbonate mineralogy and the presence of the tooth and socket hinge and will be informally referred to as 'articulated'. The former Inarticulata has been split up into two subphyla, Linguliformea and Craniaformea; thus neither group possesses a tooth and socket hinge. Members of these groups can also be referred to as inarticulated brachiopods. The main synapomorphy of the Linguliformea is the presence of an organophosphatic shell, while the craniaformean skeleton is composed of calcium carbonate. The craniaformeans can be further distinguished due to a specialized cemented life mode that abandons the pedicle attachment of the Rhynchonelliformea and most linguliformeans. In addition to the distinctive mineralogy among brachiopods, linguliformeans have a different larval life mode, as their larvae develop planktotrophically, or with a relatively long pelagic stage, as compared to the lecithotrophic larvae of the rhynchonelliformeans and the craniaformeans. In terms of Recent relative diversity, the rhynchonelliformeans are far more abundant than members of the other two subphyla, which are only represented by a handful of genera in today's oceans.

Subphylum Linguliformea

With a geological range spanning the whole Phanerozoic, the linguliformeans represent the earliest brachiopods, as well as some of the earliest benthic organisms with a mineralized skeleton, as species from the Order Paternida are known from rocks from the early Tommotian in Siberia. The subphylum is generally accepted as the clade representing a sister group to all other brachiopods. They are represented today by three genera, the most renowned of which is the burrowing genus *Lingula*. Linguliformeans quickly gained a worldwide distribution, occupying both inner and outer shelf environments, and after trilobites, they can be considered the second most important part of benthic assemblages throughout the Cambrian and early Ordovician (Bassett *et al.* 1999).

Order Acrotretida

The acrotretids are minute (1-2 mm diameter for adult shell) linguliformean brachiopods. Synapomorphies include a laminated organophosphatic shell characterized by a columnar microstructure in the secondary layer and overlain by a chitinous periostracum, a small (up to 300 μm diameter) larval shell with pitted micro-ornament, and a small pedicle foramen exclusive to the pedicle valve.

Acrotretids first appear in Atdabanian rocks (Rowell and Krause, 1973), and reach their maximum diversity (of 29 genera within six families) by the end of the Cambrian, during which time the group occupied both shelf and basinal environments and achieved a near cosmopolitan distribution (Bassett *et al.* 1999). Throughout the early Ordovician, acrotretid habitats diversified to include near-shore and inner-shelf carbonate mounds (Krause and Rowell, 1975), as well as disaerobic abyssal plains, in which a few genera seemed to share a symbiotic relationship with hexactinellid sponges (Lenz, 1993). From the Arenig onwards, disparity and diversity dropped, and after the late Ordovician (Ashgill) mass extinction, only 4 monogeneric families remained. Very little work has been done on Silurian and Devonian acrotretids, but representatives are known from Oklahoma (Ireland, 1961), northern and eastern Canada (von Bitter and Ludvigsen, 1979), and south eastern Australia (Brock *et al.* 1995), and they are believed to have gone extinct by the Frasnian-Fammenian boundary (Ludvigsen, 1974).

Acrotretid Morphology

The Shell

The acrotretid skeleton is made up of two distinct valves; the dorsal or brachial valve, which is generally subcircular in outline and shallowly convex, and the ventral or pedicle valve, which is cone shaped to varying degrees and is pierced by the pedicle foramen. Each valve possesses its corresponding larval valve at its apex. The structure of shell itself is organized into the primary, secondary, and possibly tertiary layers composed of calcium phosphate lamellae penetrated by layers of organic material. Based on comparison with Recent lingulates, Ushatinskaya (1990) estimated that at least 50% of the shell was organic. The two organophosphatic layers are overlain by an organic periostracum. Preservation of the organic parts of the shell must have required early diagenetic phosphatization, as in *Lingula*; it is estimated that without organic preservation the whole shell would be lost in only a few days (Emig, 1990).

Periostracum

The thin, organic (likely chitinous) layer covering the shell of all brachiopods is called the periostracum. It is secreted by epithelial cells and consists of a thin (2 μm) layer of flat rectangles separated by low ridges (Ushatinskaya, 1990). Poulsen (1971) described this layer as the outer layer of the shell and suggested that the periostracum would not preserve in acrotretids due to its organic nature. Ushatinskaya (1990) suggested that Poulsen's outer layer was in fact a very well preserved cast of the periostracum.

The periostracum is present at the larval stage of acrotretids and it has been suggested that a vesicular nature of this organic layer may leave remnant pits on the underlying larval shell (Biernat and Williams, 1970).

Primary Layer

The primary shell layer, referred to as the outer layer by Pelman (1987), lies directly beneath the periostracum and is made up of a single lamina about 1-1.5 µm thick (Ushatinskaya, 1990). Its outer surface is penetrated by small (0.5 µm), blind apertures that may correspond to small out-pocketings of the lower surface of the periostracum. The surface of the primary layer possesses a fibrous or spongy appearance, similar to the organic layer in lingulids. Ushatinskaya (1990) suggested that this appearance indicates an organic composition for this layer, however, this is not universally accepted.

Secondary Layer

Referred to as the inner layer by Poulsen (1971) and the middle layer by Pelman (1987) the secondary shell layer forms the main part of the acrotretid shell. It consists of a framework of calcium phosphate lamellae (from 2-5 µm) separated by hollow spaces (up to 20-30 µm) and connected by round pillars or columellae (2-5 µm thick). The lamellae are double walled with the two layers parallel to one another and separated by a narrow slit. The surfaces of the lamellae are smooth and have a spongy appearance, which Ushatinskaya (1990) suggested might indicate an organic nature.

Holmer (1989) described the secondary layer of some Middle Ordovician acrotretids from Sweden in great detail, and concluded that there is an interfamilial disparity based on the arrangement of this layer. Holmer (1989) introduced two terms to describe this difference: in a 'columnar layer' the lamellae are connected to one another by hollow, apatitic rods or pillars lying perpendicular to the lamellae, while in a 'camerate layer', thin perpendicular walls connect the lamellae and form irregular honeycomb patterns. In the families Acrotretidae, Torynelasmatidae, and Scaphelasmatidae, the secondary layer is camerate, while in Ephippelasmatidae, Biernatidae, and possibly Eoconulidae it is columnar. In a columnar layer, the lamellae themselves may be oriented perpendicular or at an angle to the shell surface, and both of these orientations occur in the Ephippelasmatidae, Biernatidae, and Eoconulidae. The morphology of septal denticles is highly variable, even intraspecifically, and Ushatinskaya (1990) suggested that this variability might be due to a cartilaginous-like origin for the denticles.

Tertiary Layer

Holmer (1989) proposed the existence of a tertiary layer in the Acrotretidae and Torynelasmatidae. Located internal to the camerate layer, it consists of a columnar layer similar to the innermost layers of the Biernatidae secondary layer, in which the columns lie perpendicular to the shell surface. This layer is often difficult to distinguish from the secondary layer, so this distinction may be artificial.

Larval Shell

The larval shell of acrotretids is located at the apex of each adult valve and possesses a shape similar to its corresponding adult valve. The pedicle larval valve is conical with an average height of 150 µm and, except in the scaphelasmatids, possesses a pedicle foramen (Holmer, 1989). It has a mean diameter of approximately 100-300µm, and in composed of a single layer 2-3 µm thick (Ushatinskaya, 1990). The larval valves lack the concentric growth lines seen in adult acrotretids. Instead, the microstructure consists of round, flat-bottomed pits that may or may not cross cut one another (Biernat and Williams, 1970; Ludvigsen, 1974). In some genera, these pits represent a single uniform size (2-5 µm), while in others, there exists a series of very small pits (0.5 µm) occupying the space between the larger ones.

There has been much debate on the nature and origin of these pits (i.e. Biernat and Williams, 1970; Ludvigsen, 1974; von Biter and Ludvigsen, 1979; Popov *et al.*, 1982). This will be discussed in chapter four of this work.

Anatomy

Most of what is known about the acrotretid soft anatomy must be derived from the uniformitarian inference of homology with the living inarticulated brachiopods, as well as from the interpretation of skeletal structures such as muscle scars and median septa.

Pedicle

The pedicle of inarticulated brachiopods is a hollow outgrowth of the ventral body wall that connects with the coelom of the body cavity. This differs from that of articulated brachiopods, which possess a solid pedicle that is completely excluded from the body cavity.

The pedicle foramen in acrotretids is located at or near the apex of the pedicle valve, and is a completely enclosed aperture. Although Chuang (1974) suggested that this foramen may have functioned as an exhalent siphon in acrotretids, recent consensus holds that it did in fact house the pedicle (Rowell, 1977; Popov and Ushatinskaya, 1992). The foramen is very small in size (~50 μm), which likely translates into a small pedicle size for the acrotretids.

Ontogenetically, the foramen forms from the dethyrial opening (Bassett *et al.* 1999). This transformation occurs in the early post-larval stage of Cambrian acrotretids, but in some younger forms it may occur even earlier, resulting in an enclosed foramen at the planktonic larval stage (Popov and Ushatinskaya, 1992; Lazarev, 1992).

Muscles

The articulated brachiopods possess a tooth and socket hinge arrangement and are therefore limited in terms of relative valve movement. However, a rigid hinge is absent in the inarticulated forms, as the valves are held together by muscles only and valve movement is controlled by these two muscle groups. Anterior and posterior pairs of adductor muscles close the valves. The oblique muscles, of which there can be a variable number, assist in closure, but function mainly in opening the valves and controlling their relative longitudinal and rotary movement.

Reconstruction of the musculature in acrotretids has been interpreted two different ways, based upon homology with Recent genera *Discinisca* (Williams and Rowell, 1965) or *Lingula* (Popov, 1992). In Williams and Rowell's (1965) model, the anterior and posterior adductor muscles of discinids are responsible for the major muscle scars found in acrotretid shells. The posterior adductor produces the cardinal scars and apical pits in the pedicle valve, and the cardinal scars in the brachial valve, and the anterior adductors insert at the apical process in the pedicle valve and the antero-central scars in the brachial valve. Popov (1992) interpreted the musculature in a conical acrotretid pedicle valve as that of a 'rolled up' linguloidean pedicle valve. As such, in the acrotretid pedicle valve, central cardinal scars would have been formed by equivalents of the linguloidean transmedian and anterior lateral muscles, the apical pits by the umbonal muscles, and the outside lateral, middle lateral and central muscles would have attached at the apical process. In the brachial valve of acrotretids, the cardinal scars would be formed by the transmedian, outside lateral and/or middle lateral, the antero-central scars by the central and anterior lateral muscles, and the linguloidean umbonal would attach at the median buttress. As an inclusion of this reconstruction, Popov and Holmer (1996) suggested that acrotretids likely possessed fewer muscles than lingulids, and that their muscles may have been tendonized due to the unequal muscle fields in each valve.

Lophophore

The brachiopod lophophore is a ciliated organ consisting of two arms (brachia) of tentacles arranged symmetrically around the mouth, which extend from the anterior body wall into the mantle cavity. It functions mainly in food gathering, inhalant/exhalant current generation, and respiration, and is composed mostly of a hyaline cartilage-like connective tissue. In the inarticulated brachiopods, the position and form of the lophophore are maintained mainly by muscles and hydrostatic pressure, while in some articulated forms it has the added support of a calcareous structure called the brachidium.

During ontogeny, the lophophore increases in both size and complexity, and while size is limited by the growth of the organism itself, complexity is largely unrestrained and is the most important factor in increasing lophophore surface area. Brachiopod larvae and early juveniles possess a trocholophe, which is the least complex of the lophophore patterns, as the brachia are arranged in a simple crescent around the mouth (Rudwick, 1962). The next stage in complexity is the schizolophe pattern, in which the tips of the trocholophe brachia have curved towards the mouth. This type of lophophore occurs in most juveniles and in the adults of a few groups, including the living discinid *Pelagodiscus* (Emig, 1992). The schizolophe pattern is generally only sufficient to handle the pumping costs for a brachiopod of up to 4 mm in diameter (Rowell and Grant, 1987), so a larger surface area, and therefore a more convoluted lophophore pattern is required for larger brachiopods. The acrotretid lophophore was likely of the schizolophe arrangement, as it would be energetically sufficient for these minute brachiopods; however, there may have been major modification of the lophophore in the acrotretids with high conical pedicle valves. For most of the inarticulated brachiopods, the lophophore is arranged in a spirolophe, which is an extension of the schizolophe pattern in that each brachium spirals dorsally away from the other.

Body and Organ Systems

In generalized brachiopod morphology, the body occupies a very small proportion of the space between the valves (Rudwick, 1970). The rest of the space is occupied mainly by the lophophore. In addition, there are two mantle lobes that extend from the body and line the inner surface of the shell. The space between these (and therefore anterior to the body) is referred to as the mantle cavity. The body is separated from the mantle cavity by a body wall, within which the organs and muscles are suspended in a coelomic fluid.

Cell Size

The structure of cells in the acrotretids has never been reported. Possible cellular structures have been identified in new species from the Ordovician of Argentina (presented in chapter two of this work). They are polygonal in shape and average 14-16μm in diameter (roughly 3 times the size of the large pits).

Ontogeny

Larval Development of Marine Invertebrates

Benthic, marine invertebrates utilize various developmental modes from egg to adult. These modes have been divided into three broad categories: brooding, demersal, and pelagic development (Thorson, 1950; Mileikovsky, 1971). Pelagic development can be further divided into a dichotomy involving feeding or trophic type. Lecithotrophic development involves a very short pelagic stage (2-3 days) where relatively few larvae receive nourishment from the yolk reserves in their large eggs. In contrast, larvae with planktotrophic development are in the water column for a longer period of time (5 days to one year), and grow by feeding themselves on the plankton. They also hatch in much higher numbers, and from much smaller eggs.

Brooding, demersal, and lecithotrophic development take place within, or very near the parent organism, and therefore require high levels of parental care for a low number of offspring. Planktotrophic development, on the other hand, involves the effective abandonment of millions of offspring into the water column for relatively long periods of time. Therefore, larvae that are brooded or are fed by their eggs are released into the water column larger, and perhaps better prepared for life than the smaller planktotrophs. Indeed, the mortality rate of larvae in the plankton has been estimated at 99% (Thorson, 1950). Fortunately, however, fecundity (or number of offspring) in organisms with this type of larvae is high enough that the few surviving percent (estimated as low as 0.00005-0.0001% for some invertebrate populations; Jablonski and Lutz, 1983) are enough for the population to persist.

In living forms, pelagic (especially planktotrophic) larval development is most abundant, occurring within at least 70% of today's species (Mileikovsky, 1971). However, there tends to be a distribution gradient from low to high latitudes, and from shallow to deep waters, in which the other types of larval development replace the planktotrophic type (Thorson, 1950). Although these non-pelagic forms are hampered by low fecundity, low dispersion, and high reproductive output per offspring, they seem to be better adapted for life in the extreme conditions presented by high latitude and deep water. Valentine and Jablonski (1983, p.1055) suggested that this is due to the fact that at high latitudes the selective advantage favours organisms that are effectively "fortified" against seasonal variations (as opposed to low latitudes, which favour high fecundity).

The pelagic larvae of benthic marine invertebrates comprise the meroplankton of the zooplankton community, which are those plankters that are only temporary residents in the euphotic zone (upper 70m of the sea; Johnson, 1957). They may remain in the water column from 2 days up to a year feeding on phytoplankters, other zooplankters, or organic detritus (Day and McEdwards, 1984). Most larvae fall within the microplankton size category (2 μm-2 mm), which is small enough that they inhabit a life of low Reynolds (Re) numbers characterized by laminar flow, strong viscous forces, and relatively no inertial forces (Purcell, 1977, Vogel, 1981). Although spines may help, at such low Re, shape probably has very little to do with buoyancy (Chia *et al.*, 1984; Speyer and Chatterton, 1989), and there seem to be no major restrictions on the shape of plankton.

Like the rest of the plankton, larvae are relatively weak swimmers, but the need to catch food has brought about some morphological adaptations for swimming. For example, cilia form an effective swimming organelle for larvae of small size (<1 mm), while the larger forms may utilize muscular locomotion in the form of swimming appendages (Chia *et al.*1984). With these adaptations, larvae have been known to reach speeds of 60 cm/min, which allows them to have some control over their vertical distribution (Mileikovsky, 1973).

One of the major advantages conferred by planktotrophic development is the ability for these pelagic larvae to disperse long distances, thereby increasing the range of their species (Thorson, 1950). Although it is possible that organisms may "over disperse" and thereby miss suitable settlement sites (Strathmann, 1980), in the majority of cases, the advantage of dispersal remains an important by-product of planktotrophic development. In fact, various diffusion studies and hypotheses maintain that larvae in the plankton for six weeks can be carried as far as 500 km, on a moderate current speed of 0.5 km/h (Scheltema, 1977).

Brachiopod Larvae

In the living brachiopods, the articulated forms develop through lecithotrophy and the inarticulated forms through planktotrophy. However, this may not have always been the case. Although these larvae do not possess a shell, and it is therefore difficult to ascertain their developmental life mode, analyses based on dispersal studies and evidence of their wide distribution imply that a planktotrophic development may have existed in their evolution (Rong *et al.* 1995). If they were planktotrophic in the past, it is possible that the shift to lecithotrophy may have corresponded to major extinction events, such as that of the Ordovician-Silurian (Chatterton and Speyer, 1989) and Permo-Triassic boundaries (Valentine and Jablonski, 1983).

Larvae of Living Inarticulated Brachiopods

All of the Recent inarticulated brachiopod groups are known to possess a shelled planktotrophic larval stage in their development, and are generally highly dispersed because of it (Scheltema, 1977). The larval stage can be defined as the period from the appearance of two lophophore filaments until settlement, the end of which is represented on the adult shell as a small growth-disturbance ring (Holmer, 1989). Various larval stages of lingulids and discinids can be collected from within a meter of the water surface (Chuang, 1968). The larval valves are secreted simultaneously by both mantles (Williams and Rowell, 1965). In lingulids, development consists of an increase in shell size, and in the number of cirrus pairs, but in discinids, the number of cirrus pairs remains constant at four, so that only shell size can be used as an indicator of developmental phase (Chuang, 1968). The lophophore of the discinid *Pelagodiscus* is described as a horizontal disk with a centrally placed mouth on the ventral side, and nine lophophoral processes radiating out (Chuang, 1968, p. 266). The larval lophophore is used to swim and to feed (Strathmann, 1978). In the larvae of *Glottidia*, "the lophophore is extended through the gape of the shell and the small brachiopod moves through the water oriented vertically" (Paine, 1963, p. 196).

Lingulids possess a shelled embryo as well as shelled larvae, whereas only the larvae of the discinids are shelled (Chuang, 1977). The larval shells of both lingulids and discinids are between 300-400 μm in diameter, and the exterior shell surfaces are generally smooth, with the exception of one thin-shelled fossil lingulid, *Paterula*, which possess a distinctly pitted larval shell (Holmer, 1986). The transition from a pelagic larva to a benthic adult is not accompanied by major internal restructuring, or metamorphosis in the inarticulated brachiopods (Paine, 1963; Strathmann, 1978). Lingulids generally have a longer planktotrophic stage than discinids, with up to 20 days in *Glottidia* and only six days in *Pelagodiscus* (Chuang, 1977; Holmer, 1989). The fecundity of *Glottidia* can reach to 47000 eggs (Paine, 1963). Geographical distribution of the living inarticulated brachiopods is comparable to that of other organisms with planktotrophic development, constituting a maximum distribution at low latitudes, which decreases towards the poles (Jablonski and Lutz, 1983).

Acrotretid Larvae

Through a uniformitarian argument, it is safe to postulate that acrotretid larvae were planktotrophic, and likely developed in a pattern similar to that of Recent inarticulated forms, using their trocholophe lophophore to swim and feed. As mentioned above, the acrotretid larval valve is ornamented with flat-bottomed, circular pits. It has been suggested that the pitting on the larval shells aided these brachiopods in buoyancy (i.e. Biernat and Williams, 1970; von Bitter and Ludvigsen, 1979), and that increasing complexity in the pitting patterns may correspond to a longer time in the water column. It is this theory, in conjunction with a set of other characters unique to the acrotretids, which will provide the major framework for the hypotheses presented in the fourth chapter of this work.

Summary

Acrotretid brachiopods are found in a wide variety of paleoenvironments and geographical locations, and were a prolific part of the fauna of the Early Paleozoic. In the following chapters, new species will be described from locations and time periods not previously sampled for acrotretids, and the habitat for some of the morphologically enigmatic forms will be discussed.

CHAPTER 2

Acrotretids from the Ordovician of Argentina

INTRODUCTION

Acrotretid brachiopods reach the height of their diversity and disparity in the Ordovician, but they have never been described from rocks of this age in Argentina. Previous studies on the Cambrian and Ordovician Precordillera of northwestern Argentina have included groups such as trilobites (i.e. Baldis and Blasco, 1973; Chatterton *et al.*, 1997, 1999; Edgecombe *et al.*, 1998, 1999; Waisfeld *et al.*, 2001), sponges (i.e. Carrera, 1997, 2000), and conodonts (i.e. Albanesi, 1998; Albanesi et al., 1998; Huenicken and Barnes, 1998). Only recently have acrotretids been studied in this area, resulting in the descriptions from the Cambrian of the northern Argentina Precordillera (Holmer *et al.*, 1999). This work marks the first description of acrotretid brachiopods from the Ordovician of Argentina.

LOCALITIES AND BIOGEOGRAPHY

All of the material was collected and processed by B.D.E Chatterton during numerous field excursions to the following localities:

Rio Gualcamayo

Two localities were sampled from strata in the Gualcamayo Formation east of the Rio Gualcamayo in the northwest of San Juan province (north of Jachal). The Gualcamayo Formation consists of dark, marly limestones, mudstones, and shales overlying the lighter limestone of the San Juan Formation (Benedetto *et al.* 1986). Two Lower Ordovician (Arenig) horizons (RGO-7 and RGO-F) from this section were found to contain acrotretids (Fig. 2-1). Both are located in the lower half of the Gualcamayo Formation, which has been interpreted by Astini (1995) to be a transitional area from the shelf environment of the San Juan Formation to a sloping ramp environment. Details of the stratigraphy can be found in Waisfeld *et al.* (2001).

RGO-7: This horizon is located 25 m above the base of the Rio Gualcamayo East section, and contains the highest diversity of all the horizons considered in this work, with seven acrotretid species: *Conotreta delfina*, *Hisingerella gualcamayensis*, *Ottenbyella aguada*, *Undiferina viracocha*, *Eoconulus talathus*, *Torynelasma suecicum*, and *Scaphelasma naithum* (Fig. 2-2).

RGO-F: This horizon is located 2 m below RGO-7 in the same section, yet contains only a single species, *Hisingerella gualcamayensis* (Fig. 2-2).

Ponon Trehue (PT-1)

This locality contains Middle Ordovician (Llanvirn) limestones, and is located southwest of San Rafael, near Ponon Trehue in Mendoza province (Fig. 2-1). Detailed descriptions of this area can be found in Baldis and Blasco (1973) and Bordonaro et al. (1996). The horizon examined here yielded three new acrotretid species, including *Conotreta tiburona*, *Tasbulakia ondata*, and *Scaphelasma naithum*, of which *T. ondata* is the most abundant (Fig. 2-2).

Las Aguaditas (LA 0-10cm)

Located southwest of San Jose de Jachal, in the San Juan province, this locality contains Middle Ordovician (Llanvirn) carbonates from the Las Aguaditas Formation. The Las Aguaditas Formation is up to 300 m thick, and is made up of calcareous and marly beds with intercalated breccias (Chatterton *et al.* 1998). The samples studied in this work were taken from thin-bedded mudstones and shales just above the boundary with the San Juan Formation (Fig. 2-1). A detailed description of this area, including a locality map and stratigraphic columns, can be found in Chatterton *et al.* (1998) and Waisfeld *et al.* (2001). The sampled horizon contains three acrotretid species, *Conotreta tiburona, Scaphelasma naithum* and *Eoconulus talathus*, of which *C. tiburona* is the most abundant (Fig. 2-2).

SYSTEMATIC PALEONTOLOGY

Subphylum LINGULIFORMEA Williams *et al.*, 1996
Class LINGULATA Gorjanskij and Popov, 1985
Order ACROTRETIDA Kuhn, 1949
Superfamily ACROTRETOIDEA Schuchert, 1893

Family ACROTRETIDAE Schuchert, 1893

DIAGNOSIS: "Ventral valve conical, more rarely convex; ventral pseudointerarea commonly bisected by intertrough or interridge; pedicle foramen circular or elongate oval, apical or immediately posterior to beak; foramen completely or partly within larval shell; apical process variable, usually with muscle platform directly anterior to pedicle tube; dorsal interior usually with median septum or ridge; median buttress commonly present; cardinal muscle fields usually thickened, becoming wider anterocentrally" (Holmer and Popov, 2000: 103). *Lower Cambrian-Silurian (Wenlock).*

Genus CONOTRETA Walcott, 1889

TYPE SPECIES *Conotreta rusti* Walcott, 1889 from the Middle Ordovician Trenton Group of New York State.

DIAGNOSIS: "Ventral valve high conical; ventral pseudointerarea procline to somewhat apsacline, usually with interridge; foramen enclosed within larval shell; dorsal pseudointerarea with wide median groove; apical process forming low ridge along anterior slope of valve; apical pits shallow, placed directly lateral to apical process; ventral mantle canals pinnate; dorsal median septum high, triangular, usually with anterior denticles or spines; dorsal interior with large cardinal muscle scars and median buttress" (Holmer, 2000). *Ordovician (Arenig-Ashgill).*

REMARKS: The type species of *Conotreta*, *Conotreta rusti* Walcott is poorly known, as Walcott (1889) illustrated only three pedicle valves. This had created some confusion about the strict diagnosis of this genus, leading to a very wide morphological range and including up to thirty species. In order to clear this up, Holmer (2000) provided a re-examination of syntypes and topotypes of *C. rusti* Walcott and reassessed the list of included species. The two species assigned to *Conotreta* in this work are done so using Holmer's (2000) redescription of the genus.

SPECIES INCLUDED: *C. rusti* Walcott, 1889, Upper Ordovician (Caradoc) of New York State; *C. apicalis* Cooper, 1956, Middle Ordovician of Alabama; *C. multisinuata* Cooper, 1956, Middle Ordovician of Tennessee and Virginia; *C. mica* Gorjanskij, 1969, Lower-Middle Ordovician of Nevada; Middle Ordovician of Poland, Estonia, Sweden and Russia; *C. lepton* Williams and Curry, 1985, Lower Ordovician (Arenig) of Ireland; *C. siljanensis* Holmer, 1989, Middle Ordovician of Sweden and Newfoundland; *C. shidertensis* Popov and Holmer, 1994, Upper Ordovician of south Ural Mountains; *C. chernovi* Popov, 2000, Upper Ordovician (Upper Caradoc) of Kazakhstan; *C. millardensis* Popov, Holmer and Miller, 2002, Lower Ordovician (Tremadoc) of Utah; *C. delfina* new species, Lower Ordovician (Arenig) of Argentina; *C. tiburona* new species, Middle Ordovician (Llanvirn) of Argentina.

UNDESCRIBED SPECIES: *C.* sp. Krause and Rowell, 1975, Lower-Middle Ordovician of Nevada; *C.* sp. Termier and Monad, 1978, Lower Ordovician (Tremadoc) of Turkey; *C.* sp. Williams and Curry, 1985, Lower Ordovician (Arenig) of Ireland.

Conotreta delfina new species

Plate 2-1, Figures 1-16

ETYMOLOGY: From 'delfin' the Spanish for dolphin, with reference this larval valve's likeness to the head of a bottle-nosed dolphin in lateral view.

HOLOTYPE: CEGH-UNC 19581, brachial valve (Pl. 2-1; Figs. 1, 2, 4, 7, 14).

MATERIAL AND OCCURRENCE: 9 brachial valves and 7 pedicle valves from Lower Ordovician (Arenig) strata of the Gualcamayo Formation (RGO-7).

DIAGNOSIS: *Conotreta* with relatively large size; single set of larval pits; height-to-width ratio of 70%; median septum with single denticle; pedicle valve with flattened procline pseudointerarea and narrow interridge; short external pedicle tube; apical process broad with flattened margins.

DESCRIPTION: The shell is a large, high cone in outline marked by fine concentric growth lines. The secondary shell layer consists of pillar–like rods and horizontal lamellae (Pl. 2-1, Fig. 15).

The brachial valve is relatively large at 1.7 mm in length (Range: 1.45-1.9 mm, N=9) and 1.9 mm in width (Range: 1.8-2.0 mm), giving it a subcircular outline, as the length is 88% of the width (Pl. 2-1, Figs. 1, 4, 5). It is slightly convex in lateral view (Pl. 2-1, Fig. 2). The larval valve is a small circle, with a mean diameter of 0.21 mm (Range: 0.2-0.22 mm), only 11% of the total valve width (Pl. 2-1, Figs. 2, 6). It is ornamented with a single series of round, concave pits 0.01-0.022 mm in diameter that overlap slightly.

Internally, the brachial valve possesses a long, narrow pseudointerarea with anacline propareas separated by a shallow median groove (Pl. 2-1, Fig. 2). The length of the pseudointerarea is 13% of its width, and the complete structure extends for 44% of the total valve width. The median buttress is low and gives rise to a triangular septum that extends for 62% of the total valve length, beginning slightly posterior to the anterior margin of the cardinal muscle scars (Pl. 2-1, Figs. 2, 3, 6). The maximum height of the septum is located at the valve midlength and its height is roughly 37% of its length. Although the septum is poorly preserved or broken in this material, it is possible to discern a single rod with denticle located on the ventral margin of the median septum (Pl. 2-1, Fig. 6). The muscle scars, located posterolateral to the median buttress, are subcircular and are large, each averaging 15% of the total valve width (Pl. 2-1, Fig. 1).

The pedicle valve is a high cone (H:W 72%), and is 1.35 mm high (Range: 1.3-1.46 mm, N=7), with the greatest height slightly anterior to the apex (Pl. 2-1, Figs. 7, 8, 10-16) , 1.88 mm wide (Range: 1.71-2.0 mm) and 1.56 mm long (Range: 1.42-1.77). The pseudointerarea is catacline to slightly procline with a low, narrow interridge, giving it a flattened appearance laterally (Pl. 2-1, Figs. 10, 13). It extends for 48% of the total valve width. The larval valve (Pl. 2-1, Fig. 11) is a rounded cone 9% of the total valve height (0.17 mm, Range: 0.12-0.2 mm) and 9% of the valve width (0.2 mm, Range: 0.17-0.21 mm). It possesses a short external pedicle tube ending in a posteroventrally directed foramen (Pl. 2-1, Fig. 10, 11, 16) with a 0.04 mm diameter (Range: 0.034-.0046). There is a small bump slightly anterior to the pedicle tube, which constitutes the highest point of the valve (Pl. 2-1, Fig, 11). The larval pits are of similar size and shape to those of the brachial valve (Pl. 2-1, Fig. 14). Internally, the apical process is a trapezoidal shaped swelling with flattened sides, anterior to the foramen (Pl. 2-1, Figs. 8, 12). The muscle scars are small, circular depressions located internal and lateral to the interridge (Pl. 2-1, Fig. 8).

DISCUSSION: *Conotreta delfina* is most similar to *Conotreta mica* Goryanskij from the Llandeilo of Sweden (Holmer, 1989). Both species have 1) a weak interridge 2) a broad apical process with flattened margins 3) a median septum that begins posterior to the anterior margin of the muscle scars and 4) a single set of overlapping larval pits. *C. delfina* differs from *C. mica* in the possession of 1) a shorter median septum with a single denticle 2) a pedicle valve with a flatter pseudointerarea and 3) a distinct, short external pedicle tube. *C. delfina* reaches a larger maximum size than the other species in this genus.

Conotreta tiburona new species

Plate 2-2, Figures 1-17; Plate 2-3, Figures 1-6

ETYMOLOGY: After 'tiburon' the Spanish for shark, with reference to dorsal fin-like appearance of the median septum.

HOLOTYPE: CEGH-UNC 19586, brachial valve (Pl. 2-2, Figs. 1-4, 6, 12, 15).

MATERIAL AND OCCURRENCE: 20 pedicle valves from the Middle Ordovician (Llanvirn) near Ponon Trehue (PT-1); 30 brachial valves and 37 pedicle valves from Middle Ordovician (Llanvirn) strata of the Las Aguaditas Formation (LA 0-10cm).

DIAGNOSIS: *Conotreta* with two sets of larval pits; small dorsal muscle scars; median septum with two denticles; pedicle valve height 60% of width; distinct interridge; short external pedicle tube; apical process wide with rounded margins.

DESCRIPTION: The shell is a short cone in outline with fine concentric growth lines. It possesses a secondary shell layer consisting of many alternating layers of pillar–like rods and horizontal lamellae (especially evident in the structure of the apical process; Pl. 2-2, Figs. 13-14).

The brachial valve (Pl. 2-2, Figs. 1, 3) is 1.39 mm in length (Range: 1.29-1.45 mm, N=30) and 1.64 mm in width (Range: 1.5-1.72 mm). It is subcircular in outline with a length 84% of the width (Range: 82-86%), and is only slightly convex in lateral view (Pl. 2-2, Fig. 2). The larval valve is circular (Pl. 2-2, Fig. 6), with a mean diameter of 0.225 mm (Range: 0.2-.0235 mm), approximately 14% of the total valve width. It is ornamented with two series of round, concave pits that interrupt or cross cut slightly (Pl. 2-2, Fig. 16). The large pits have a diameter of 0.012-0.028 mm and are surrounded by small pits 0.0061-0.0084 mm in diameter.

Internally, the brachial valve possesses a relatively short, narrow pseudointerarea (Pl. 2-2, Fig. 4) that extends for 37% of the total valve width and has a length 20% of its width. The propareas are slightly anacline and are separated by a shallow median groove (Pl. 2-2, Fig. 2). The median buttress is well developed and gives rise to a triangular septum (Pl. 2-2, Fig. 2) possessing a single ventral rod with secondary denticle variously developed as a small bump (Pl. 2-2, Fig. 12). The septum height is 44% of its length, with the maximum height located anterior to the midlength, and it extends from slightly anterior to the anterior margin of the cardinal muscle scars for 67% of the total valve length. The muscle scars, located posterolateral to the median buttress, are small and subrounded, and each average 7% of the total valve width (Pl. 2-2, Fig. 1).

The height of the pedicle valve (Pl. 2-2, Figs. 7-11) is 60% of its width, and is 0.83 mm high (Range: 0.77-0.88 mm, N=57), 1.36 mm wide (Range: 1.28-1.41 mm) and 1.13 mm long (Range: 1.09-1.2). The pseudointerarea is procline with a strong interridge, and extends for 50% of the total valve width. The interridge is slightly less prominent in the Ponon Trehue (Pl. 2-3, Figs 1-3, 5) material as compared to that of Las Aquaditas (Pl. 2-2, Figs 5, 7, 9). The larval valve (Pl. 2-2, Fig. 10) is a rounded cone 13% of the total valve height (0.17 mm, Range: 0.12-0.2 mm), and possesses a short external pedicle tube extending from a small bump and ending in a posteroventrally directed foramen with a 0.036 mm diameter (Range: 0.034-.0039). The larval pits are of similar size and shape to those of the brachial valve (Pl. 2-2, Fig. 15). Internally, the apical process is a rounded swelling anterior to the foramen (Pl. 2-2, Fig. 5; Pl. 2-3, Figs. 5-6), which is made up of a series of horizontal lamellae alternating with vertical pillars in the secondary shell layer (Pl. 2-2, Figs. 13-14). The muscle scars are small, circular depressions located internal and lateral to the interridge (Pl. 2-2, Fig. 5; Pl. 2-3, Fig. 5).

DISCUSSION: *Conotreta tiburona* differs from *Conotreta delfina*, the other Argentine species described above, based on the possession of 1) a more rounded apical process, 2) a distinct interridge, 3) a shorter dorsal pseudointerarea, and 4) a shorter median septum that begins anterior to the anterior margin of the muscle scars. *C. tiburona* is similar to *Conotreta lepton* Williams and Curry, from the Lower Ordovician (Arenig) of Ireland

(Williams and Curry, 1985). Both species have shorter cones than is typical for the genus, with a height to width ratio of 60% in *C. tiburona* and only 47% in *C. lepton* (compared with 75% for most *Conotreta* species). In addition, both species have a short external pedicle tube ending in a posteroventrally directed foramen; however, the Argentine species differs in the possession of 1) a shorter median septum with up to two denticles, 2) a broad apical process with rounded margins, and 3) a distinct interridge.

Genus HISINGERELLA Henningsmoen, 1948

TYPE SPECIES: *Atrypa nitens Hisinger,* 1837, from the Middle Ordovician of Sweden.

DIAGNOSIS: "Shell subcircular with short, weakly convex posterior margin; ventral pseudointerarea procline to apsacline with interridge; foramen forming short tube, enclosed within larval shell; dorsal valve flattened, somewhat sulcate; dorsal pseudointerarea orthocline to anacline with wide median groove; apical process vestigial to absent; dorsal interior with raised cardinal muscle fields, divided by broad median buttress; dorsal median septum triangular with single upper septal rod." (Holmer and Popov, 2000: 112). *Ordovician (Arenig-Ashgill).*

REMARKS: In assigning the Argentine material to *Hisingerella*, the above diagnosis must be amended to include a spinose median septum. Although this material may represent a new monotypic genus, the author is reluctant to erect one until further species can be isolated.

SPECIES INCLUDED: *Conotreta hetera* Percival, 1978, Upper Ordovician of Australia; *H. nitens* Holmer 1986, Middle Ordovician of Sweden; *H. billingensis* Holmer, 1989, Middle Ordovician of Sweden; *H. unguicula* Holmer, 1989, Middle Ordovician of Sweden; *H. gualcamayensis* new species, Lower Ordovician of Argentina.

Hisingerella gualcamayensis new species

Plate 2-4, Figures 1-16; Plate 2-5, Figures 1-12.

ETYMOLOGY: After the locality Rio Gualcamayo.

HOLOTYPE: CEGH-UNC 19592, brachial valve (Pl. 2-4, Figs. 1, 2, 4).

MATERIAL AND OCCURRENCE: 209 brachial valves and 317 pedicle valves from Lower Ordovician (Arenig) strata of the Gualcamayo Formation (RGO-7 and RGO-F).

DIAGNOSIS: *Hisingerella* with long external pedicle tube with bulbous base; wide shelf-like apical process; and median septum with short, variously directed spines.

DESCRIPTION: The shell is a high, recurved cone in outline with a micro-ornament consisting of fine concentric growth lines, and possesses a secondary shell layer consisting of pillar–like rods and horizontal lamellae (Pl. 2-5, Figs. 10-11).

The brachial valve is 1.03 mm in length (Range: 0.98-1.05 mm, N=209) and 1.16 mm in width (Range: 1.15-1.18 mm). It is subcircular in outline (Pl. 2-4, Figs. 1, 3, 9) with a length 86% of the width (Range: 85-87%), and is slightly sulcate (Pl. 2-4, Fig. 13). The larval valve (Pl. 2-4, Figs. 6, 10) is circular, with a mean diameter of 0.214 mm (Range: 0.2-0.22 mm), approximately 18% of the total valve width. It is ornamented with two series of round, concave pits (Pl. 2-4, Fig. 16). The large pits have a diameter of 0.014-0.026 mm and are surrounded by small pits 0.0029-0.0057 mm in diameter.

Internally, the brachial valve possesses a triangular shaped pseudointerarea with anacline propareas that are separated by a deep, wide median groove (Pl. 2-4, Figs. 2, 4). It extends for 43% of the total valve width. It has a slightly convex anterior margin and a length to width ratio of 27%. The median buttress is low and gives rise to a triangular septum possessing up to three denticles variously directed off of its anterior margin (Pl. 2-4, Figs. 1-2, 5, 8). The septum height is 48% of its length, with the maximum height located anterior to the midlength, and it extends from parallel with the anterior margin of the cardinal muscle scars for 56% of the total valve length. The muscle scars, located posterolateral to the median buttress, are ovate and each average 12% of the total valve width (Pl. 2-4, Fig. 5).

The pedicle valve (Pl. 2-4, Figs. 7, 10-11; Pl. 2-5, Figs. 1, 2-3) is almost as high as it is wide (H:W 96%), and is 1.23 mm high, with the greatest height at the apex (Range: 1.22-1.26 mm, N=317), 1.28 mm wide (Range: 1.23-1.33 mm) and 1.13 mm long (Range: 1.09-1.17). The pseudointerarea is procline (Pl. 2-4, Figs. 10-12; Pl. 2-5, Figs. 1, 3, 5, 9) with a strong interridge, and extends for 46% of the total valve width. The larval valve Pl. 2-4, Fig. 14; Pl. 2-5, Figs. 4, 6, 8) is 14% of the total valve height (0.17 mm, Range: 0.12-0.2 mm) and 16% of the valve width (0.2 mm, Range: 0.17-0.21 mm) and consists of restriction at its margin (at the interface with the adult valve), followed by a slight bulge extending into a long external pedicle tube and ending in a circular foramen 0.036 mm in diameter (Range: 0.33-0.4 mm) that is directed posteroventrally. The external pedicle tube is marginally longer in specimens from RGO-7 (i.e. Pl. 2-5, Fig. 4). The larval pits are of similar size and shape to those of the brachial valve (Pl. 2-5, Fig. 12). Internally, the apical process is a low, wide shelf anterior to the foramen, which extends into a thin internal pedicle tube (Pl. 2-4, Figs. 12, 15; Pl. 2-5, Fig. 5). The secondary shell structure of the apical process consists of a series of alternating pillars and lamellae (Pl. 2-5, Figs. 10-11). The muscle scars are elongate depressions located internal and lateral to the interridge (Pl. 2-4, Figs. 12, 15).

DISCUSSION: *Hisingerella gualcamayensis* is the oldest species assigned to this genus. It is most similar to *Hisingerella billingensis* Holmer from the Llandeilo of Sweden (Holmer, 1989). Both species have a long external pedicle tube and a wide median groove, but these features are longer and wider, respectively, in *H. gualcamayensis*. In addition, the median septum of *H. gualcamayensis* differs from that of *H. billingensis* Holmer in the possession of short spines. The apical process of *H. gualcamayensis* is different from all others observed in the genus, as it is a wide shelf-like ridge anterior to the foramen.

Genus OTTENBYELLA Popov and Holmer, 1994

TYPE SPECIES: *Ottenbyella carinata* (original designation: *Acrotreta carinata*, Moberg and Segerberg, 1906) from the Lower Ordovician of Norway (redescribed by Popov and Holmer, 1994).

DIAGNOSIS: "Ventral valve highly conical with maximum height at beak; ventral pseudointerarea invariably procline, with distinct interridge, external pedicle tube very short, dorsal valve flattened, broadly sulcate; dorsal pseudointerarea wide but short, broadly subtriangular; apical process small and low; ventral *vascular lateralia* well developed, straight; dorsal median ridge very low; median buttress poorly developed; dorsal cardinal muscle fields small and short, transversely elongate suboval in outline" (Holmer and Popov, 2000: 115-117). *Ordovician (upper Tremadoc-Arenig).*

Ottenbyella aguada new species

Plate 2-6, Figures 1-17.

ETYMOLOGY: After the prehistorical Aguada civilization that occupied the Andes in northern Argentina.

HOLOTYPE: CEGH-UNC 19601, brachial valve (Pl. 2-6, Figs. 4-5).

MATERIAL AND OCCURRENCE: 6 brachial valves and 5 pedicle valves from Lower Ordovician (Arenig) strata of the Gualcamayo Formation (RG0-7).

DIAGNOSIS: *Ottenbyella* with apical process low to vestigial; foramen directed posteriorly; interridge well developed; brachial median septum low ridge initiating below median buttress.

DESCRIPTION: The shell is a large, high cone in outline marked by fine concentric growth lines. The secondary shell layer consists of pillar–like rods and horizontal lamellae (Pl. 2-6, Fig. 14). Cells are hexagonal in shape, 0.014 mm in diameter (Pl. 2, Fig. 17)

The brachial valve is flattened in lateral view (Pl. 2-6, Figs. 2, 5) and subcircular in outline (Pl. 2-6, Figs. 1, 3, 4), with a length to width ratio of 85%. The valves are 1.27 mm in length (Range: 1.0-1.57 mm, N=6) and 1.5 mm in width (Range: 1.07-1.7 mm) (note: all of the recovered brachial valves were broken, so some of the dimensions have been estimated). The larval valve is circular (Pl. 2-6, Figs. 6, 9), with a mean diameter of 0.22 mm (Range: 0.19-0.29 mm), only 18% of the total valve width. It is ornamented with a single series of round, concave pits 0.01-0.02 mm in diameter, which overlap slightly (Pl. 2-6, Fig. 17).

Internally, the brachial valve possesses a wide pseudointerarea, triangular in outline with a straight anterior margin (Pl. 2-6, Figs. 1, 4). The orthocline propareas are separated by a wide median groove with a rounded posterior margin (Pl. 2-6, Fig. 2). The length of the pseudointerarea is 19% of its width, and the complete structure extends for 58% of the total valve width. The median buttress is low and wide, and drops into a low median ridge that originates anterior to the muscle scars (Pl. 2-6, Fig. 5). The height and length of the median ridge is unknown, but there seems to be no indication that it ever reaches the height of a septum. The muscle scars, located posterolateral to the median buttress, are circular and each average 18% of the total valve width (Pl. 2-6, Figs. 1, 4).

All of the pedicle valves found were broken in a similar location, anterior to the larval valve, so the dimensions were estimated. The pedicle valve (Pl. 2-6, Figs. 7, 8, 10-13) is a wide cone (H:W 72%), and is 1.35 mm high (Range: 1.3-1.46 mm, N=8), 1.18 mm wide (Range: 1.71-2.0 mm) and 1.56 mm long (Range: 1.42-1.77). The pseudointerarea is procline with a distinct interridge (Pl. 2-6, Figs. 11-13). It extends for 48% of the total valve width. The larval valve (Pl. 2-6, Fig. 16) is a rounded cone 9% of the total valve height (0.17 mm, Range: 0.12-0.2 mm) and 9% of the valve width (0.2 mm, Range: 0.17-0.21 mm). It possesses a short external pedicle tube ending in a posteriorly directed foramen with a 0.05 mm diameter (Range: 0.044-0.056). The highest point of the valve is slightly anterior to the foramen. (Pl. 2-6, Fig, 11). Internally, the apical process is low (Pl. 2-6, Fig. 7, 15) to vestigial (Pl. 2-6, Fig. 10), and the muscle scars are elongate ridges (Pl. 6, Figs. 1, 10).

DISCUSSION: Only the type species *Ottenbyella carinata* Moberg and Segerberg is known for this genus, and *Ottenbyella aguada* is comparable based on 1) the flattened lateral profile of the brachial valve 2) the presence of a low median ridge (rather than a high septum) 3) the wide, triangular pseudointerarea with a wide median groove 4) the procline pedicle pseudointerarea with a distinct interridge and 5) the short external pedicle tube. The main differences between these two species are the low apical process and posteriorly directed foramen in the pedicle valves of *O. aguada*.

Genus TASBULAKIA Popov, 2000

TYPE SPECIES: *Tasbulakia tenuis* Popov, 2000, from the Upper Ordovician (Ashgill) Bestyube Formation, Kazakhstan.

DIAGNOSIS: "Shell high, slightly apsaconical with poorly defined ventral pseudointerarea divided medially by weak intertrough; pedicle foramen facing posteroventrally, enclosed within larval shell; dorsal valve gently convex with narrow anacline pseudointerarea, which does not exceed half of the maximum valve width; larval shell finely pitted with rounded pits of slightly varying size, postlarval shell smooth; ventral interior with short internal pedicle tube supported anteriorly by thin, ridge like apical process; dorsal interior with high, triangular median septum bearing up to five septal rods projecting anteriorly as long spines; cardinal muscle fields small, rounded, situated on raised platforms; cardinal buttress wide, slightly raised anteriorly" (Popov, 2000: 425). *Ordovician (Arenig-Ashgill).*

SPECIES INCLUDED: *T. tenuis* Popov, 2000, Upper Ordovician (Ashgill) of Kazakhstan; *T. ondata* new species, Middle Ordovician (Llanvirn) of Argentina.

REMARKS: With the inclusion of the new Argentine species, the diagnosis for this genus must be amended to include a ventral pseudointerarea with a weakly defined interridge.

Tasbulakia ondata new species

Plate 2-7, Figures 1-16; Plate 2-8, Figures 1-16.

ETYMOLOGY: After 'onda' the Spanish for wave, in reference to the appearance of the denticles on the median septum.

HOLOTYPE: CEGH-UNC 19606, brachial valve (Pl. 2-7, Figs. 1-4, 6-8, 11, 14-15).

MATERIAL AND OCCURRENCE: 98 brachial valves and 117 pedicle valves from the Middle Ordovician (Llanvirn) near Ponon Trehue (PT-1).

DIAGNOSIS: *Tasbulakia* with median septum high, 2-4 anterior denticles, ventralmost of which is recurved ventrally; shallow median groove; pedicle valve height half width; apical process elongate ridge, interridge present.

DESCRIPTION: The shell is a large, wide cone in outline marked by fine concentric growth lines. The secondary shell layer consists of pillar–like rods (Pl. 2-7, Figs. 14-15; Pl. 2-8, Fig. 11) and horizontal lamellae (Pl. 2-7, Figs. 8, 11; Pl. 2-8, Figs. 7, 11-13). These alternating layers become more numerous in structures like the apical process (Pl. 2-8, Figs 7, 11-13). Cells are trapezoidal to hexagonal in shape, 0.016 mm in length (Pl. 2-8, Fig. 15).

The brachial valve is relatively large at 1.17 mm in length (Range: 0.9-1.54 mm, N=) and 1.33 mm in width (Range: 1.05-1.73 mm), giving it a subcircular outline, as the length is 88% of the width (Pl. 2-8, Figs. 1, 3). The width increases relative to the length in larger (presumably older) individuals (i.e. Pl. 2-7, Figs. 1-3; Pl. 2-8, Fig. 6), and the length to width ratio decreases to 81%. It is slightly convex in lateral view (PL. 2-7, Fig. 2). The larval valve (Pl. 2-7, Fig. 4; Pl. 2-8, Fig. 4) is circular, with a mean diameter of 0.21 mm (Range: 0.2-0.22 mm), 18% of the total valve width. It is ornamented with a single series of round, concave pits 0.012-0.02 mm in diameter, which overlap slightly (Pl. 2-8, Fig. 8).

Internally, the brachial valve possesses a long, straight pseudointerarea extending 45% of the total valve width (Pl. 2-7, Fig. 6; Pl. 2-8, Fig. 3). The anacline propareas are separated by a shallow median groove (Pl. 2-8, Fig. 2), and the total pseudointerarea length is 16% of its width. The median buttress is well developed and gives rise to a high, triangular septum that begins posterior to the anterior margin of the cardinal muscle scars, and extends for 57% of the total valve length. The maximum height of the septum is located at the valve midlength and its height is 55% of its length. The anterior margin of the septum possesses two to four denticles supported by parallel rods seen running through the septum (i.e. Pl. 2-8, Fig. 16). In the smaller individuals, there are only two denticles, but the ventral margin already displays a sharp incline. In the larger individuals, the three denticles on the anterior margin are directed anteriorly, while the denticle running along the ventral margin points ventrally, giving the median septum the appearance of a wave about to turn into a white-cap (Pl. 2-7, Fig. 2; Pl. 2-8, Fig. 6). The muscle scars, located posterolateral to the median buttress, are large and elongate platforms, each taking up 13% of the total valve width (Pl. 2-8, Fig. 3).

The pedicle valve (Pl. 2-7, Figs. 5, 7, 9, 10; Pl. 2-8, Figs. 5, 9) is a wide, short cone (H:W 72%), and is 1.07 mm high (Range 0.4-0.1.5 mm, N=19), 1.5 mm wide (Range 0.8-2.1, N=32), and 1.3 mm long (Range: 0.7-1.77). The pseudointerarea extends for 45% of the total valve width and is strongly procline with a well-developed interridge (Pl. 2-7, Figs. 5, 7, 10). The larval valve is a rounded cone with no external pedicle tube (Pl. 2-7, Fig. 13). It is 9% of the total valve height (0.17 mm, Range: 0.12-0.2 mm) and 9% of the valve width (0.2 mm, Range: 0.17-0.21 mm). The small, circular foramen is 0.027 mm in diameter, is located posterior to the valve's highest point, and is directed posteriorly (Pl. 2-7, Figs. 5, 7). The larval pits are of similar size and shape to those of the brachial valve. Internally, the apical process is an elongate triangular ridge anterior to the foramen (Pl 2-7, Figs. 12, 16; Pl. 2-8, Fig. 5). The muscle scars are large, circular depressions located internal and lateral to the interridge (Pl. 2-7, Fig. 12; Pl. 2-8, Fig. 10, 14).

DISCUSSION: Until this work, this genus contained only the type species, *Tasbulakia tenuis* Popov, from the Ashgill of Kazakhstan (Popov, 2000), which is much younger than the Argentine species. *Tasbulakia ondata* differs from the type species in having 1) a slightly procline ventral pseudointerarea with a weakly defined interridge, rather than an intertrough, 2) a larger height to length ratio for the median septum, and 3) a maximum of four denticles as compared to five in the Kazakhstan material. *T. ondata* is placed within this genus based on similarities with the type material, including 1) the arrangement and structure of the median septum (more specifically, of the denticles), 2) the height to width ratio of the ventral valve, and 3) the ridge-like tubercle structure of the apical process.

Family EOCONULIDAE Rowell, 1965

DIAGNOSIS: "Shell asymmetrical with fine rugae; ventral valve encrusting; pedicle opening may be sealed internally; ventral pseudointerarea absent; dorsal pseudointerarea commonly absent; apical process bosslike, anterior to foramen." (Holmer and Popov, 2000: 133) *Ordovician (Arenig-Ashgill).*

Genus EOCONULUS Cooper, 1956

TYPE SPECIES: *Eoconulus rectangulatus* Cooper, 1956, from the Middle Ordovician (Llandeilo) Pratt Ferry Formation of Alabama.

DIAGNOSIS: "Dorsal valve conical, usually with subcentral apex; cardinal muscle fields of both valves generally strongly thickened" (Holmer and Popov, 2000: 133). *Ordovician (Arenig-Ashgill).*

SPECIES INCLUDED: *E. rectangulus* Cooper, 1956, Middle Ordovician of Alabama; USA; *E. transversus* Wright, 1963, Middle Ordovician of Ireland; *E. cryptomyus* Goryanskij, 1969, Middle Ordovician of Russia; *E. semiregularis* Biernat, 1973, Middle Ordovician of Poland; *E. antelopensis* Krause and Rowell, 1975, Middle Ordovician of Nevada; *E. clivosus* Popov, 1975, Middle Ordovician of Kazakhstan; *E. dyminensis* Bednarczyk and Biernat, 1978, Lower Ordovician (Arenig) of Poland; *E. robustus*

Holmer, 1989, Middle Ordovician (Llandeilo) of Sweden; *E. talathus* new species, Lower-Middle Ordovician (Arenig-Llanvirn) of Argentina.

UNDESCRIBED SPECIES: *E.* sp. of Holmer and Biernat, 2002, Lower Ordovician (Tremadoc) of Poland.

Eoconulus talathus new species

Plate 2-9, Figures 1-15

ETYMOLOGY: From 'talath', the Sindarin for plain or unadorned, with reference to the featureless interior of the brachial valve.

HOLOTYPE: CEGH-UNC 19617, brachial valve (Pl. 2-9, Figs. 4, 6, 9, 12).

MATERIAL AND OCCURRENCE: 41 brachial valves from Lower Ordovician (Arenig) strata of the Gualcamayo Formation (RG0-7); 19 brachial valves from Middle Ordovician (Llanvirn) strata of the Las Aguaditas Formation (LA 0-10cm).

DIAGNOSIS: *Eoconulus* with height nearly half the width; brachial interior lacking cardinal muscle scars.

DESCRIPTION: Only brachial valves were recovered and are all ornamented with parallel growth lines. The valve is 0.69 mm long (Range: 0.67-0.72 mm, N=60), 0.73 mm wide (Range: 0.7-0.77), and 0.36 mm high. It is a low, wide cone, subquadrate in outline with the length 95% of the width (Pl. 2-9, Figs. 1, 3, 9), and the height 45% of the width (Pl. 2-9, Figs. 2, 6, 8). The larval valve (Pl. 2-9, Figs. 11-13) is circular with a diameter of 0.19 mm (27% of the total valve width), and is located at the apex of the valve. The apex on most of the specimens is broken (Pl. 2-9, Figs. 11, 13), but two series of larval pits are still visible around the break (Pl. 2-9, Fig. 15). The large pits are discrete, round, and flat-bottomed with a diameter of 0.06-0.075 mm. In certain areas where the first layer of the larval shell is missing, the pits are manifested as round platforms (Pl. 2-9, Figs 10, 14). Clusters of small, concave pits, 0.009-0.012 mm in diameter, surround the large pits. Internally, the pedicle valve is featureless (Pl. 2-9, Fig. 4).

A single specimen from the Las Aguaditas locality possesses a small, rod-like structure extending from the posterior wall (Pl. 2-9, Figs. 5, 7). It is 0.17 mm long (25% of the valve length) and 0.04 mm wide (24% of the septum length). This structure is likely not a part of the original genetic make-up of the shell, as it is more probably an erratic shell secretion in response to an irritant.

DISCUSSION: Many authors have commented on the fact that meaningful species diagnoses within the genus *Eoconulus* are problematic, due to the fact that the morphology reflects the configuration of the environment of this cementing brachiopod (i.e. Holmer, 1989). To add to the confusion, many species are known only from their brachial valves, as the cementing pedicle valve may have been only partially mineralized in life (Krause and Rowell, 1975). This is the case for the material described here, as only brachial valves have been recovered. *Eoconulus talathus* best resembles *Eoconulus* *clivosus* Popov from the Middle Ordovician of Kazakhstan (Popov, 1975), as both species share 1) a length to width ratio of 95% and 2) a large larval valve relative to the total valve width (approximately 27%). However, the outline of *E. talathus* is more quadratic, the sides are sloped more steeply, the height to width ratio is greater, and the interior of the brachial valve is featureless.

Genus UNDIFERINA Cooper, 1956

TYPE SPECIES: *Undiferina rugosa* Cooper, 1956, from the Middle Ordovician (Llandeilo) Pratt Ferry Formation of Alabama.

DIAGNOSIS: "Ventral valve like *Eoconulus*, but higher; dorsal valve with marginal beak; dorsal pseudointerarea orthocline to anacline with median groove; dorsal interior with high, triangular median septum with rod or narrow thickened surmounting plate" (Holmer and Popov, 2000:136). *Ordovician (Arenig-Llandeilo).*

SPECIES INCLUDED: *U. rugosa*; Cooper, 1956; Llandeilo, Pratt Ferry, Alabama. *U. nevadensis*; Rowell and Krause, 1973, Llanvirn, Nevada and central Kazakhstan.

Undiferina viracocha new species

Plate 2-10, Figures 1-16.

ETYMOLOGY: After the supreme Incan god, Viracocha, whose name means sea foam.

HOLOTYPE: CEGH-UNC 19619, brachial valve (Pl. 2-10. Figs. 1, 3).

MATERIAL, LOCALITIES AND HORIZONS: 5 brachial valves and 6 pedicle valves from Lower Ordovician (Arenig) strata of the Gualcamayo Formation (RG0-7).

DIAGNOSIS: *Undiferina* with dorsal pseudointerarea strongly anacline; median septum triangular with slightly thickened ventral margin; anterocentral muscle scars prominent platforms; ventral valve truncated cone with large muscle scars internally.

DESCRIPTION: The shell is a large, biconvex, truncated cone in outline marked by thick concentric growth lines. The shell is thick and the secondary shell consists of a few layers of pillar–like rods and horizontal lamellae (Pl. 2-10, Fig. 2). Cellular structures found on the median septum and the muscle scars are polygonal with a diameter of 0.015 mm (Pl. 2-10, Fig. 13).

The brachial valve is relatively large at 1.76 mm in length (Range: 1.62-1.91 mm, N=) and 2.19 mm in width (Range: 1.94-2.38 mm). It is ovate in outline (Pl. 2-10, Fig. 1, 6), as the length is 80% of the width (Range: 79-83%), and is strongly convex in lateral view (Pl. 9, Fig 3). The larval valve (Pl. 2-10, Fig. 9) is subcircular and convex, with a mean width of 0.21 mm (Range: 0.2-0.22 mm), 9.5% of the total valve width. It is ornamented with a single series of round, concave pits 0.015-0.02 mm in diameter, which overlap slightly (Pl. 2-10, Fig. 14).

Internally, the brachial valve possesses a large, concave pseudointerarea extending 55% of the total valve width (Pl. 2-10, Figs. 1, 5). The strongly anacline propareas are separated by a deep, wide median groove (Pl. 2-10, Figs. 2, 3, 8) that has convex posterior and anterior margins. The total pseudointerarea length is 29% of its width. The median buttress is a thick, triangular boss located beneath the median groove (Pl. 2-10, Fig. 12). The median septum extends for 64% of the total valve length. It is a low ridge until slightly anterior to the valve midlength, where it extends into a triangular wedge, with its maximum height 33% of its length (Pl. 2-10, Figs. 2, 3). The cardinal muscle scars (Pl. 2-10, Fig. 16), located posterolateral to the median buttress, are large and rounded platforms, each taking up 13% of the total valve width (Pl. 1-3, 5, 8). The anterocentral muscle scars (Pl. 2-10, Figs. 1, 5, 15) are prominent circular platforms lateral to the median septum, which each average 4% of the total valve width.

The pedicle valve is a wide, truncated cone with steeply sloped sides (Pl. 2-10, Figs. 4, 7, 10). Its height (0.57 mm; Range:) is 25% of its width (2.26 mm; Range 0.8-2.4, N=32). It is subrectangular in outline with a length (1.6 mm; Range:) to width ratio of 64%. The pseudointerarea is represented as only a flattening of the posterior slope. The dorsal margin of this slope is convex (Pl. 2-10, Fig. 10), which likely provided a point of articulation with the deep brachial groove in life. The larval valve (Pl. 2-10, Fig. 11) is flattened and circular, with a mean diameter of 0.18 mm (8% of the total valve width), and is pierced by a circular foramen 0.04 mm in diameter. Internally, the apical process is absent, and the muscle scars (Pl. 2-10, Fig. 7) are large, circular platforms located posterolateral to the pedicle foramen, and comprising 12% of the total valve width.

DISCUSSION: As discussed above for *Eoconulus*, *Undiferina* presents a challenge for systematists attempting to describe and compare species, as the morphology may have closely matched whichever substrate the animal attached itself to. However, it is possible to discern features diagnostic of the genus and to measure their differences in order to recognize separate species. Of the two species previously assigned to this genus, *Undiferina viracocha* most closely resembles the type material, *Undiferina rugosa* Cooper from the Llandeilo of Alabama, which is known only from brachial valves (Cooper, 1956). Both species share 1) a similar ornamentation consisting of thick rugae 2) a length to width ratio of 80% and 3) a strongly anacline dorsal pseudointerarea with a deep, wide median groove. The Argentine material differs from *U. rugosa* in the possession of 1) a medium septum lacking a surmounting plate 2) rugae in a concentric arrangement 3) a dorsal pseudointerarea lacking anterior 'tooth-like projections' (Cooper, 1956: 263). The pedicle valve of *Undiferina nevadensis* Rowell and Krause is known from the Llanvirn of Kazakhstan (Popov and Holmer, 1994) and possesses a truncated shape similar to that of *U. viracocha*, but the latter can be differentiated due to its flat exterior lacking the small bumps seen on *U. nevadensis*.

Family SCAPHELASMATIDAE Rowell, 1965

DIAGNOSIS: "Shell biconvex to concavoconvex with straight or weakly concave posterior margin; ornament of coarse, regularly spaced rugae, lamellose peripherally; ventral pseudointerarea with widely triangular intertrough; foramen not enclosed within larval shell; apical process vestigial to absent, usually forming low projection anterior to foramen; apical pits small, directly lateral to apical process; dorsal median septum triangular, bladelike, arising near midvalve and extending almost to anterior margin, or absent; dorsal anterocentral scars directly lateral to septum" (Holmer and Popov, 2000: 122). *Middle Cambrian (Amgaian)-upper Silurian.*

Genus SCAPHELASMA Cooper, 1956

TYPE SPECIES: *Scaphelasma septatum* Cooper, 1956 from the Middle Ordovician Pratt Ferry beds, Pratt Ferry, Alabama.

DIAGNOSIS: "Ventral valve low conical to conical; ventral pseudointerarea poorly defined, procline; foramen large, oval; apical process variably developed; dorsal valve with high median septum; median buttress absent" (Holmer and Popov, 2000:122). *Ordovician (Arenig-Ashgill).*

SPECIES INCLUDED: *S. septatum* Cooper, 1956, Lower Ordovician of Ireland, Middle Ordovician of Alabama and Poland; *S. rugosum* Goryanskij, 1969, Lower Ordovician of Russia, Middle Ordovician of Sweden; S. *subquadratum* Biernat, 1973, Lower to Middle Ordovician of Poland; *S. anomalatum* Krause and Rowell, 1975, Lower-Middle Ordovician of Nevada; *S. lamellosum* Krause and Rowell, 1975, Lower-Middle Ordovician of Nevada; *S. tumidatum* Krause and Rowell, 1975, Lower-Middle Ordovician of Nevada; *S. mica* Popov, 1975, Middle Ordovician of Kazakhstan, Sweden, and Newfoundland; *S. bukowkense* Bednarczyk and Biernat, 1978, Lower Ordovician (Arenig) of Poland.; *S. pusillum* Popov, 1980, Ordovician of Kazakhstan, Middle and Upper Ordovician (upper Caradoc) of Sweden; *S. afflata* Zhang, 199, Lower-Middle

Ordovician of China; *S. hunanensis* Zhang, 1991, Lower-Middle Ordovician of China; *S. scutula* Popov, Nolvak and Holmer, 1994, Upper Ordovician of Estonia; *S. zharykensis* Popov, 2000, Upper Ordovician (Ashgill) of Kazakhstan.

UNDESCRIBED SPECIES: *S.* sp. Biernat, 1973, Upper Ordovician of Poland; *S.* sp. nov. a Holmer, 1989 Middle Ordovician of Sweden; *S.* new sp. A Robson and Pratt, 2001, Middle Ordovician of Newfoundland.

Scaphelasma naithum new species

Plate 2-11, Figures 1-15

ETYMOLOGY: From 'naith' the Sindarin (Tolkien's noble tongue) for wedge, in reference to the shape of the median septum.

HOLOTYPE: CEGH-UNC 19628, brachial valve (Pl. 2-11, Figs. 8, 9, 15).

MATERIAL AND OCCURRENCE: 6 brachial valves and 5 pedicle valves from Lower Ordovician (Arenig) strata of the Gualcamayo Formation (RG0-7); 4 brachial valves and 3 pedicle valves from the Middle Ordovician (Llanvirn) near Ponon Trehue (PT-1); 1 brachial valve and 1 pedicle valve from Middle Ordovician (Llanvirn) strata of the Las Aguaditas Formation (LA 0-10cm).

DIAGNOSIS: *Scaphelasma* with valve length over three quarters width. Pedicle valve less than half as high as wide; pseudointerarea strongly procline, intertrough shallow;

foramen ovate, half excluded from larval valve; apical process well developed anterior to foramen. Brachial valve umbonally convex, remainder flat; pseudointerarea reduced, orthocline; median septum high, wedge shaped. Adult shell highly imbricate with thin, evenly spaced lamellae; larval shell pitted with discrete series of large pits surrounded by clusters of smaller ones.

DESCRIPTION: The shell is a low, rounded, biconvex cone in outline with a micro-ornament consisting of evenly spaced concentric fila. It possesses a secondary shell layer consisting of pillar–like rods and horizontal lamellae (Pl. 2-11, Fig. 11).

The brachial valve has a straight posterior margin and is generally flattened, but with a convex umbo. It is 0.84 mm in length (Range: 0.75-0.95 mm, N=11) and 1.03 mm in width (Range 0.9-1.07). It is rounded subquadrate (Pl. 2-11, Fig. 1) in outline with the length 81% of width (Range 68-90%). The larval valve (Pl. 2-11, Fig. 10) is highly convex in lateral view and rounded subquadrate in outline, with a length 77% of the width. The width of the larval valve is 0.2 mm (Range: 0.19-0.21 mm), approximately 20% of the total valve width. It is ornamented with two series pits (Pl. 2-11, Fig. 14). The large pits are flat bottomed and have a diameter of 0.028-0.05 mm and are surrounded by small, concave pits 0.005-0.01 mm in diameter.

Internally, the brachial valve possesses a thin, orthocline pseudointerarea with a shallow median groove (Pl. 2-11, Figs. 2-3, 8-9). It extends for 55% of the total valve width and has a length 12% of its width. The median septum is a high triangular shaped wedge rounded anteriorly (Pl. 2-11, Fig. 9), extending 63% the length of the valve, with its greatest height 55% of the septum length and located anterior to the valve midlength. The muscle scars are not prominent.

The pedicle valve is 45% as high as it is wide (Range 41-48%, N=9), and is 0.46 mm high (Range: 0.4-0.75 mm), 1.02 mm wide (Range: 0.9-1.2 mm) and 0.87 mm long (Range: 0.7-0.95). The pseudointerarea is procline with a shallow intertrough running from the foramen to the posterior valve margin (Pl 2-11, Figs. 4, 6, 7). It extends for 19% of the total valve width. The larval valve (Pl. 2-11, Fig. 13) is 19% of the valve width (0.175 mm, Range: 0.16-0.2 mm). The pedicle foramen is a small oval, half excluded from larval valve and approximately 70% as wide as it is long. A single specimen from Ponon Trehue possesses a low apical process (Pl. 2-11, Figs. 6, 12) anterior to the foramen, while in all others, such a structure is absent (Pl. 2-11, Fig. 7).

DISCUSSION: This species looks similar to *Scaphelasma mica* (Holmer, 1989), except that the median septum is a much higher blade, suggestive of that of *Scaphelasma lamellosum* (Krause and Rowell, 1975). In comparison to the latter species, however, the new species possesses a more ovate pedicle foramen and much finer fila. In addition, a low apical process is present in at least one specimen of *S. naithum*, which differs from both *S. mica* and *S. lamellosum*.

Family TORYNELASMATINAE Rowell, 1965

DIAGNOSIS: "Shell with wide, straight posterior margin; ventral valve subpyramidal; ventral pseudointerarea flat, procline to apsacline, undivided; foramen enclosed within larval shell; dorsal pseudointerarea wide, poorly divided; ventral interior with low, ridgelike apical process supporting pedicle tube; dorsal valve with high, triangular median septum, commonly with variably developed surmounting platform; broad median buttress elevated above median groove; dorsal anterocentral scars absent" (Holmer and Popov, 2000: 124). *Ordovician (Arenig)-Silurian.*

Genus TORYNELASMA Cooper, 1956

TYPE SPECIES: *Torynelasma toryniferum* Cooper, 1956 from the Middle Ordovician Pratt Ferry beds, Pratt Ferry, Alabama.

DIAGNOSIS: "Ventral pseudointerarea catacline to weakly apsacline; dorsal median septum high with flat to dorsally concave surmounting platform" (Holmer and Popov, 2000: 124). *Ordovician (Arenig-lower Caradoc).*

SPECIES INCLUDED: *T. minor* Cooper, 1956, Middle Ordovician of Alabama; *T. toryniferum* Cooper, 1956, Middle Ordovician of Alabama; *T. rarum* Biernat, 1973, Lower to Middle Ordovician of Poland; *T. rossicum* Gorjanskij, 1969, Lower-Middle Ordovician of Estonia; *T. papillosum* Krause and Rowell, 1975, Lower-Middle Ordovician of Nevada; *T. suecicum* Holmer, 1989, Lower Ordovician of Argentina, Middle Ordovician of Sweden.

UNDESCRIBED SPECIES: *T.* sp. Biernat, 1973, Lower Ordovician of Poland

Torynelasma suecicum Holmer, 1989

Plate 2-12, 1-6

SYNONYMY: *Torynelasma suecicum* Holmer sp. nov.; Holmer, 1989 Figs. 28, 74A-L, 75A-K.

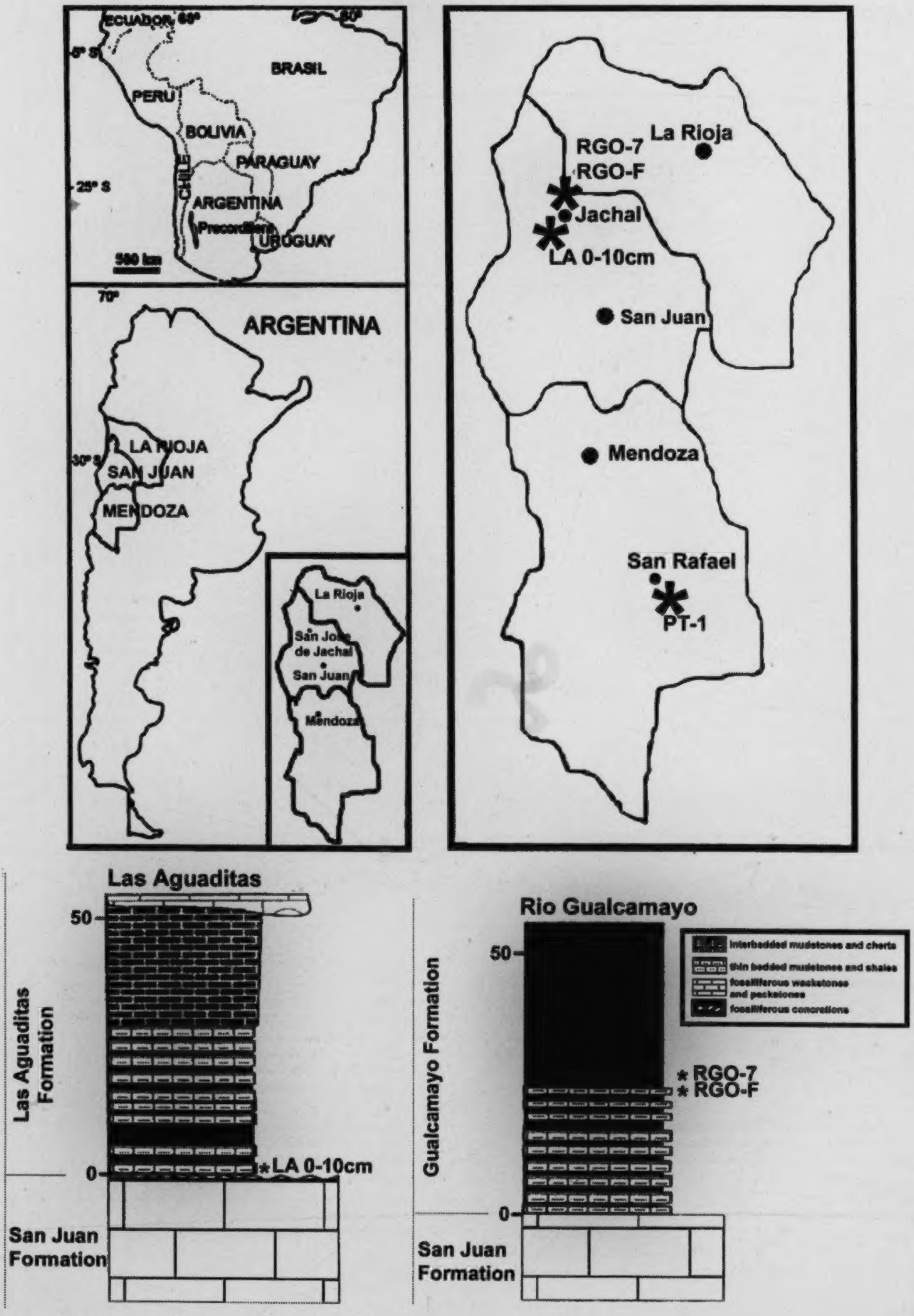
MATERIAL, LOCALITIES AND HORIZONS: 5 brachial valves and 8 pedicle valves from Lower Ordovician (Arenig) strata of the Gualcamayo Formation (RG0-7).

DIAGNOSIS: "Ventral valve with depressed apex, and wide, triangular pseudointerarea lacking interridge. Ventral interior with pedicle tube and forked median septum" (Holmer, 1989: 107).

DISCUSSION: Measurements of the Argentine material are very similar to that of Sweden. Both valves have a subtriangular outline (Pl. 2-12, Figs. 1, 4-6) with a long straight hingeline and the pedicle valve is a high cone (Pl. 2-12, Fig. 2). The length to width ratio is 74%, with the pseudointerarea extending for 67% of the total valve width and the median septum for 75% of the valve length. In all of the Argentine specimens, the median septum was either missing or broken (Pl. 2-12, Figs. 3, 4, 6), so a comparison with that of *Torynelasma suecicum* Holmer from the Middle Ordovician of Vastergotland cannot be made. However, the Lower Ordovician specimens from Argentina are similar to the Swedish material in 1) outline and lateral profile of both the brachial and pedicle valves 2) width of the brachial pseudointerarea relative to the total valve width 3) dimensions of the larval valves relative to the total valve dimensions.

Figure 2-1: Locality map and stratigraphy of the Argentine areas of study. (modified from Chatterton *et al*. 1998 and Waisfeld *et al*. 2001)

Figure 2-1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SAN JUAN
MENDOZA
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San Jose de Jachal
San Juan
Mendoza
RGO-7
RGO-F
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San Juan
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San Rafael
PT-1
Las Aguaditas
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Las Aguaditas Formation
* LA 0-10cm
San Juan Formation
Rio Gualcamayo
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Gualcamayo Formation
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thin bedded mudstones and shales
fossiliferous wackestones and packstones
fossiliferous concretions
* RGO-7
* RGO-F
San Juan Formation

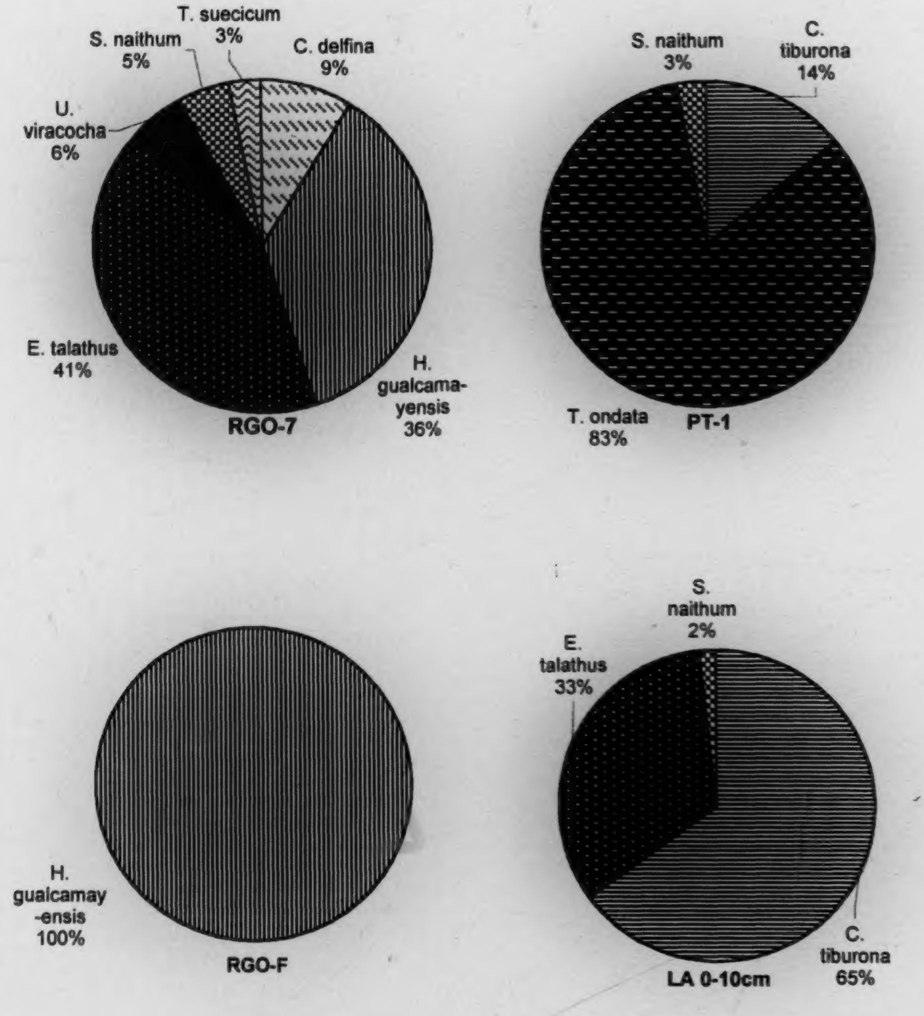

Figure 2-2: Relative species abundance for the four Argentine localities.

	Conotreta delfina	*Conotreta tiburona*	*Hisingerella gualcamayensis*	*Ottenbyella aguada*	*Tasbulakia ondata*	*Eoconulus talathus*	*Undiferina viracocha*	*Scaphelasma naithum*
Length	1.47	1.39	10.6	1.07	1.17	0.69	1.76	0.815
Width	1.71	1.49	1.2	1.1	1.2	0.73	2.19	1.02
Height	1.35	0.83	1.1	0.81	0.47	0.36	0.57	0.46
L:W (%)	85	84	87	93	88	95	80	0.8
H:W (%)	72	60	90	68	48	47	25	45
Septum % of L	62	67	56	-	57	25	64	55
Septum H:L (%)	37	44	48	-	55	25	33	59
Foramen	0.04	0.36	0.036	0.05	0.027	-	0.04	0.04
Pia % of W	44	37	43	58	45	-	55	55
Larval % of W	11	14	29	18	20	27	9	20
Pit Diameter-large	0.022	0.012-0.028	0.014-0.026	0.01-0.02	0.012-0.02	0.06-0.075	0.015-0.02	0.0275-0.05
small		0.006-0.008	0.0029-0.005			0.009-0.012		0.0005-0.001

Table 2-1: Measurements of the new species from Argentina. All measurements in mm. Pia=pseudointertarea.

Plate 2-1 *Conotreta delfina* new species from Lower Ordovician (Arenig) strata of the Gualcamayo Formation (RG0-7).

1. Interior of brachial valve; CEGH-UNC 19581; x25.
2. Oblique lateral view of brachial valve in 1; CEGH-UNC 19581; x29.
3. Oblique lateral view of brachial valve in 6; CEGH-UNC 19582; x42.
4. Exterior of brachial valve in 1; CEGH-UNC 19581; x28.
5. Exterior of brachial valve; CEGH-UNC 19582; x33.
6. Interior of brachial valve in 5; CEGH-UNC 19582; x37.
7. External view of pedicle valve; CEGH-UNC 19583; x27.
8. Internal view of pedicle valve; CEGH-UNC 19584; x27.
9. Close up of brachial larval valve in 4; CEGH-UNC 19581; x29.
10. Posterior view of pedicle valve in 7; CEGH-UNC 19583; x92.
11. Close up of pedicle larval valve in 16; CEGH-UNC 19583; x172.
12. Internal view of apical area of broken pedicle valve; CEGH-UNC 19585; x59.
13. Posterior view of pedicle valve in 8; CEGH-UNC 19584; x34.
14. Close up of larval shell margin in 9; CEGH-UNC 19581; x920.
15. Close up of secondary shell structure in 12; CEGH-UNC 19585; x5110.
16. Lateral view of pedicle valve in 7; CEGH-UNC 19583; x36.

Plate 2-1

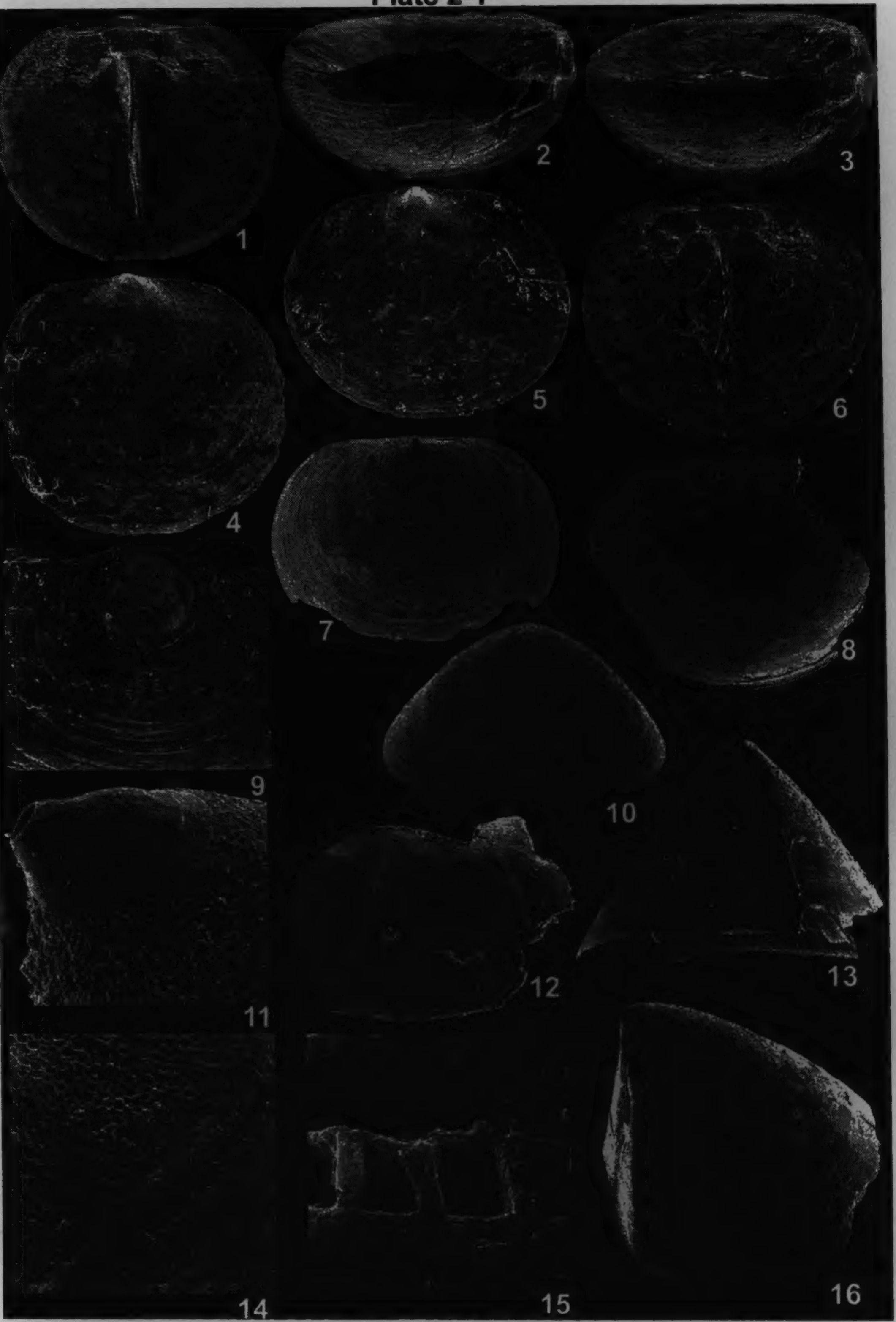
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Plate 2-2 *Conotreta tiburona* new species from Middle Ordovician (Llanvirn) strata of the Las Aguaditas Formation (LA 0-10cm).

1. Internal view of brachial valve; CEGH-UNC 19586; x25.
2. Oblique lateral view of brachial valve in 1; CEGH-UNC 19586; x31.
3. External view of brachial valve in 1; CEGH-UNC 19586; x31.
4. Close up of posterior area of brachial valve in 1; CEGH-UNC ; x43.
5. Internal view of pedicle valve; CEGH-UNC 19587; x34.
6. Close up of brachial larval valve in 3; CEGH-UNC 19586; x137.
7. External ventral view of pedicle valve; CEGH-UNC 19588; x36.
8. Posterior view of pedicle valve in 7; CEGH-UNC 19588; x36.
9. Lateral view of the pedicle valve in 7; CEGH-UNC 19588; x40.
10. Close up of pedicle larval valve in 9; CEGH-UNC 19588; x140.
11. Fragment of pedicle valve broken through apical process; CEGH-UNC 19589; x45.
12. Close up of broken denticle in median septum in 2; CEGH-UNC 19586; x1150.
13. Section of broken pedicle valve in 11 showing lamellae and pillars of secondary shell layer; CEGH-UNC 19589; x920.
14. Lateral view of broken pedicle valve in 11, showing laminated secondary shell structure in the apical process; CEGH-UNC 19589; x135.
15. Close up of pitting on the brachial larval valve in 3; CEGH-UNC 19586; 920.
16. Close up of larval pitting on pedicle valve in 11 showing an area where most of the fine pits have been obliterated; CEGH-UNC 19589; x920.
17. Close up of cellular structures on the apical process in 11; CEGH-UNC 19589; x920.

Plate 2-2

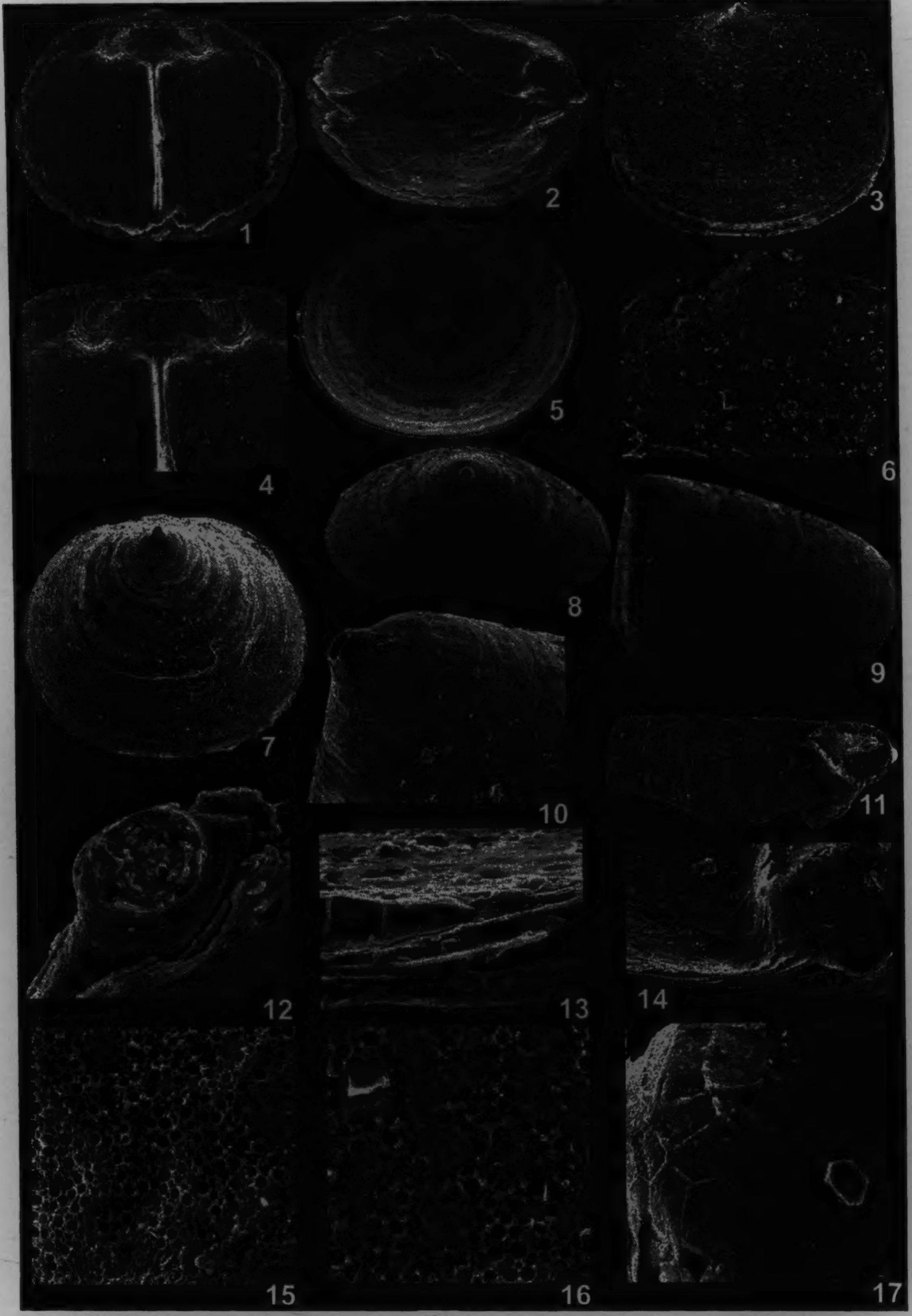
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Plate 2-3 *Conotreta tiburona* new species from the Middle Ordovician (Llanvirn) near Ponon Trehue (PT-1)

1 Superior view of pedicle valve; CEGH-UNC 19590; x40.
2 Posterior view of pedicle valve; CEGH-UNC 19591; x39.
3 Lateral view of pedicle valve in 1; CEGH-UNC 19590; x46.
4 Close up of larval valve in 1; CEGH-UNC 19590; x150.
5 Internal view of pedicle valve in 1; CEGH-UNC 19590; x43.
6 Close up of apical area in 5; CEGH-UNC 19590; x124.

Plate 2-3

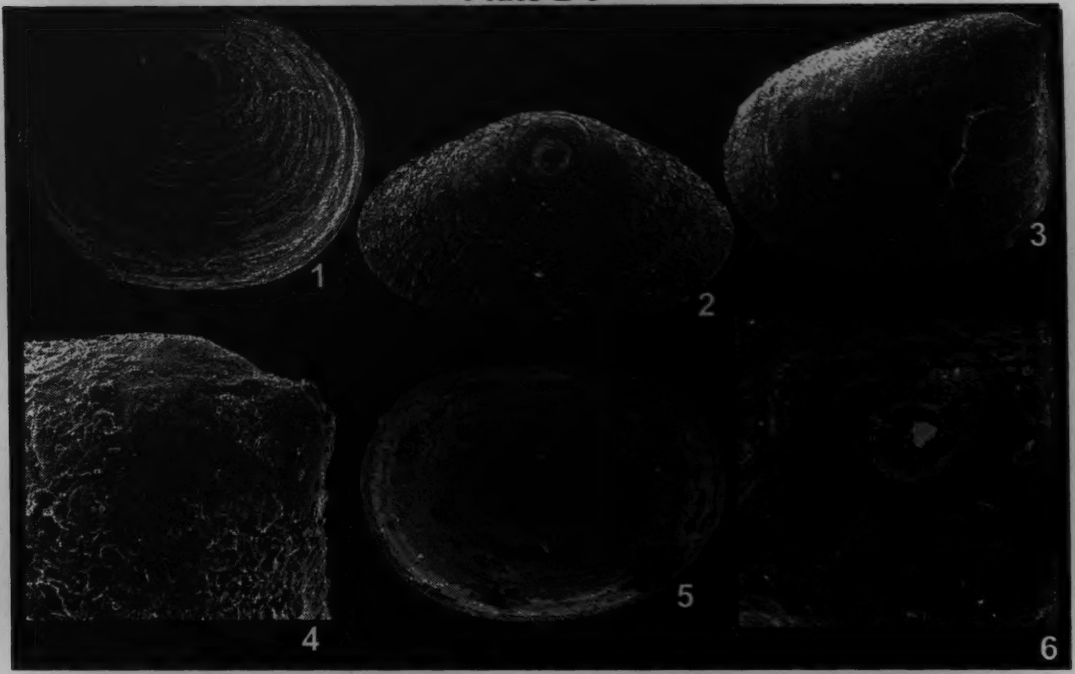

Plate 2-4 *Hisingerella gualcamayensis* new species from Lower Ordovician (Arenig) strata of the Gualcamayo Formation (RG0-F).

1. Internal view of brachial valve; CEGH-UNC 19592; x43.
2. Oblique lateral view of brachial valve in 1; CEGH-UNC 19592; x47.
3. External view of brachial valve; CEGH-UNC 19593; x46.
4. Close up of posterior area of brachial valve in 1; CEGH-UNC 19592; x51.
5. Internal view of brachial valve; CEGH-UNC 19594; x42.
6. Close up of larval valve of brachial valve in 3; CEGH-UNC 19593; x115.
7. Superior view of pedicle valve; CEGH-UNC 19595; x38.
8. Oblique lateral view of brachial valve in 5; CEGH-UNC 19594; x48.
9. External view of brachial valve in 5; CEGH-UNC 19594; x46.
10. Posterior view of pedicle valve in 7; CEGH-UNC 19595; x41.
11. Lateral view of pedicle valve in 7; CEGH-UNC 19595; x28.
12. Internal view of pedicle valve in 7; CEGH-UNC 19595; x40.
13. Close up of brachial larval valve in 9; CEGH-UNC 19594; x158.
14. Close up of pedicle larval valve in 7; CEGH-UNC 19595; x115.
15. Oblique view of pedicle interior in 12; CEGH-UNC 19594; x44.
16. Close up of larval pitting on brachial valve in 3; CEGH-UNC 19593; x1500.

Plate 2-4

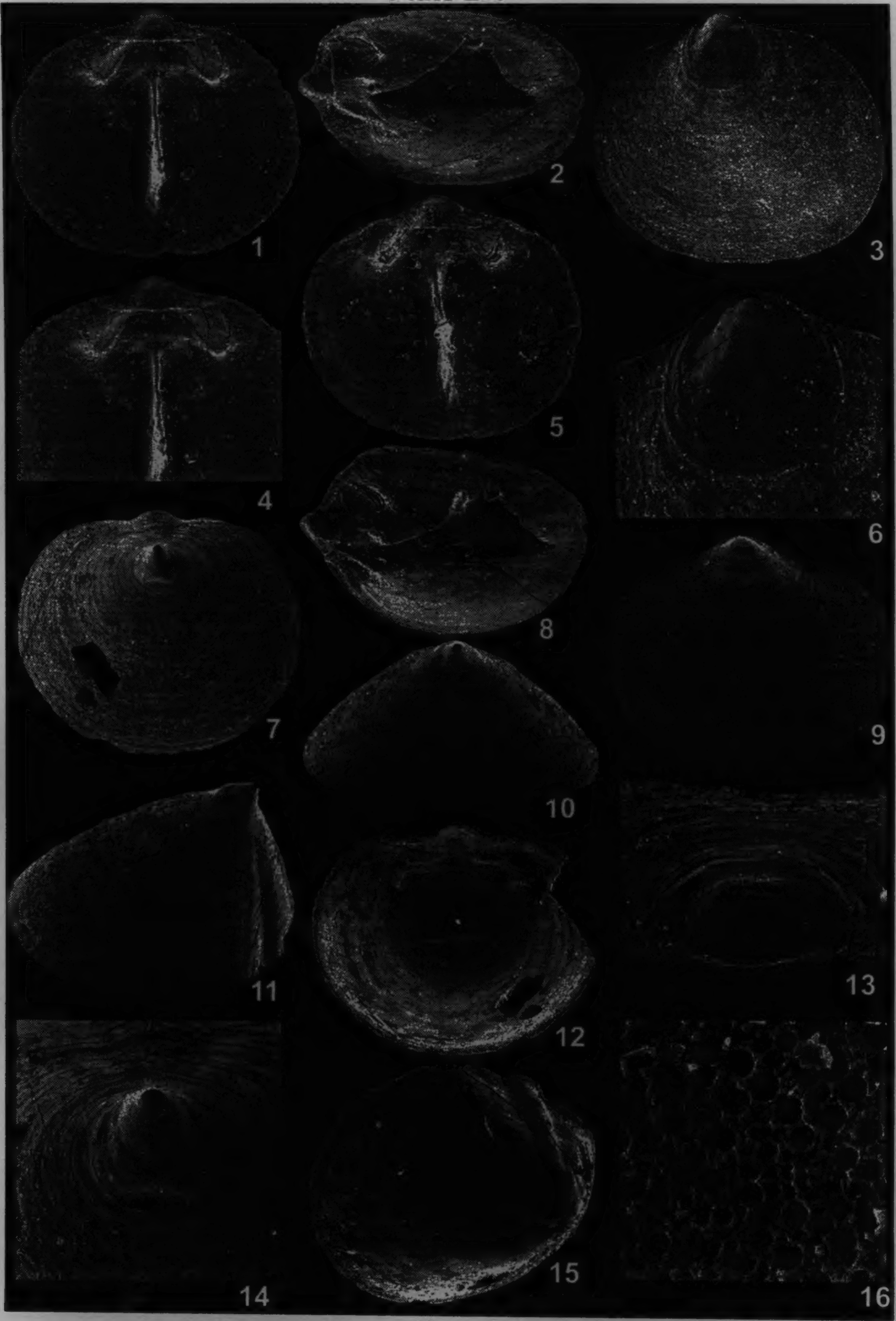
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Plate 2-5 *Hisingerella gualcamayensis* new species from Lower Ordovician (Arenig) strata of the Gualcamayo Formation (RG0-7).

1. Lateral view of pedicle valve; CEGH-UNC 19596; x59.
2. Superior view of pedicle valve; CEGH-UNC 19597; x39.
3. Lateral view of pedicle valve in 2; CEGH-UNC 19597; x48.
4. Close up of larval valve in 2; CEGH-UNC 19597; x118.
5. Internal view of pedicle valve in 1; CEGH-UNC 19596; x43.
6. Close up of larval valve in 2; CEGH-UNC 19597; x170.
7. Internal view of broken pedicle valve; CEGH-UNC 19598; x33.
8. Close up of pedicle larval valve in 9; CEGH-UNC 19596; x191.
9. Posterior view of pedicle valve in 1; CEGH-UNC 19596; x27.
10. Close up apical area in 7, showing internal pedicle tube and apical process; CEGH-UNC 19598; x57.
11. Cross section of apical process in 10, showing laminated secondary shell structure; CEGH-UNC 19598; x230.
12. Close up of pitting on the pedicle larval valve in 3, showing two pit series; CEGH-UNC 19597; x1643.

Plate 2-5

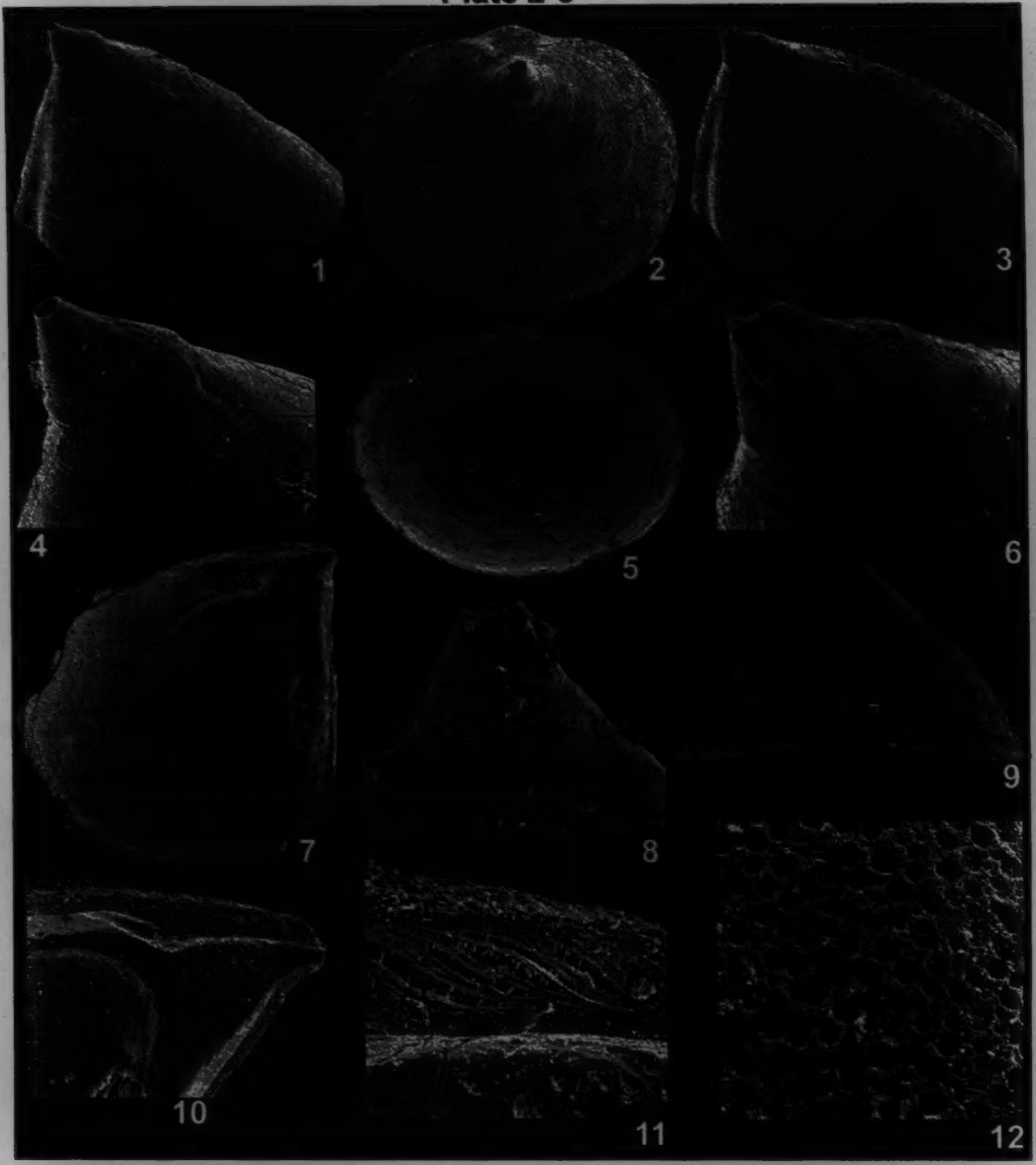
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Plate 2-6 *Ottenbyella aguada* new species from Lower Ordovician (Arenig) strata of the Gualcamayo Formation (RG0-7).

1. Internal view of brachial valve; CEGH-UNC 19599; x36.
2. Oblique lateral view of brachial valve in 1; CEGH-UNC 19599; x36.
3. External view of brachial valve; CEGH-UNC 19600; x48.
4. Internal view of brachial valve; CEGH-UNC 19601; x39.
5. Oblique lateral view of brachial valve in 4; CEGH-UNC 19601; x43.
6. Posterior view of brachial valve in 3; CEGH-UNC 19600; x48.
7. Internal view of pedicle valve; CEGH-UNC 19602; x38.
8. Superior view of pedicle valve; CEGH-UNC 19603; x45.
9. Close up of larval valve in 6; CEGH-UNC 19600; x171.
10. Internal view of pedicle valve; CEGH-UNC 19604; x37.
11. Lateral view of pedicle valve in 10; CEGH-UNC 19604; x48.
12. Posterior view of pedicle valve in 8; CEGH-UNC 19603; x44.
13. Lateral view of relatively complete pedicle valve; CEGH-UNC 19605; x50.
14. Section of broken pedicle valve in 7, showing lamellae of secondary layer alternating with pillars; CEGH-UNC 19602; x480.
15. Close up of apical area of pedicle valve in 7; CEGH-UNC 19602; x70.
16. Close up of larval valve in 12; CEGH-UNC 19603; x91
17. Close up of pitting on the brachial larval valve in 9; CEGH-UNC 19600; x1548.

Plate 2-6

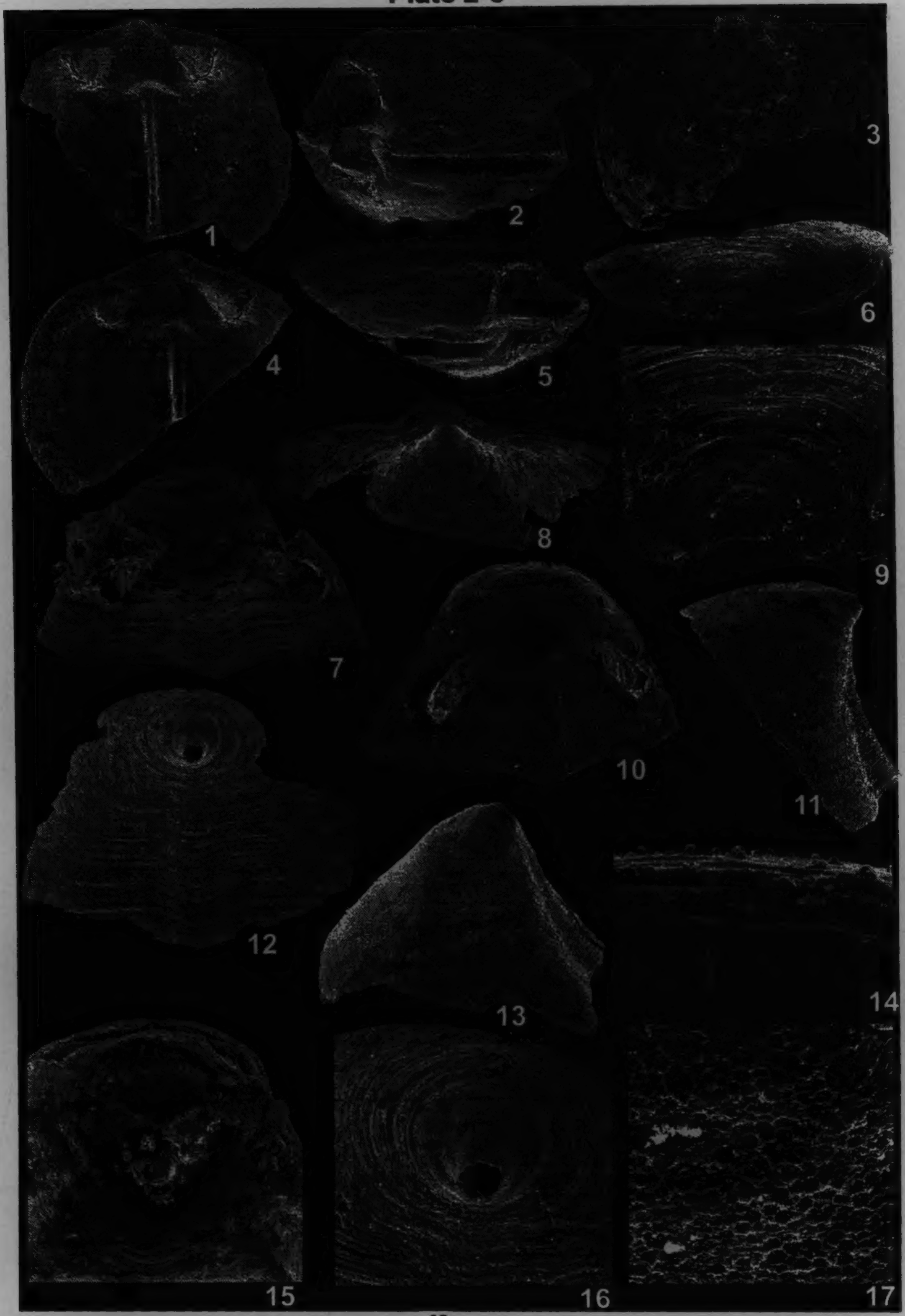
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Plate 2-7 *Tasbulakia ondata* new species from the Middle Ordovician (Llanvirn) near Ponon Trehue (PT-1)

1. Exterior of large brachial valve; CEGH-UNC 19606; x23.
2. Oblique lateral view of brachial valve in 1; CEGH-UNC 19606; x29.
3. Internal view of brachial valve in 1; CEGH-UNC 19606; x24.
4. Close up of larval valve in 1; CEGH-UNC 19606; x 92.
5. Lateral view of pedicle valve; CEGH-UNC 19607; x43.
6. Close up of posterior area in 3; CEGH-UNC 19606; x33.
7. Oblique posterior view of pedicle valve in 5; CEGH-UNC 19607; x39.
8. Close up of exfoliated larval valve in 1; CEGH-UNC 19606; x342.
9. Superior view of pedicle valve in 5; CEGH-UNC 19607; x37.
10. Posterior view of pedicle valve in 5; CEGH-UNC 19607; x57.
11. Close up of exposed section of larval valve in 8, showing lamellae of the secondary shell layer; CEGH-UNC 19606; x1840.
12. Internal view of pedicle valve in 5; CEGH-UNC 19607; x39.
13. Close up of larval valve in 5; CEGH-UNC 19607; x110.
14. Rod-like pillars in exfoliated section of larval valve in 4; CEGH-UNC 19606; x920.
15. Close up of pillars in 14; CEGH-UNC 19606; x3433.
16. Close up of apical process in 12, showing cellular structures; CEGH-UNC 19607; x134.

Plate 2-7

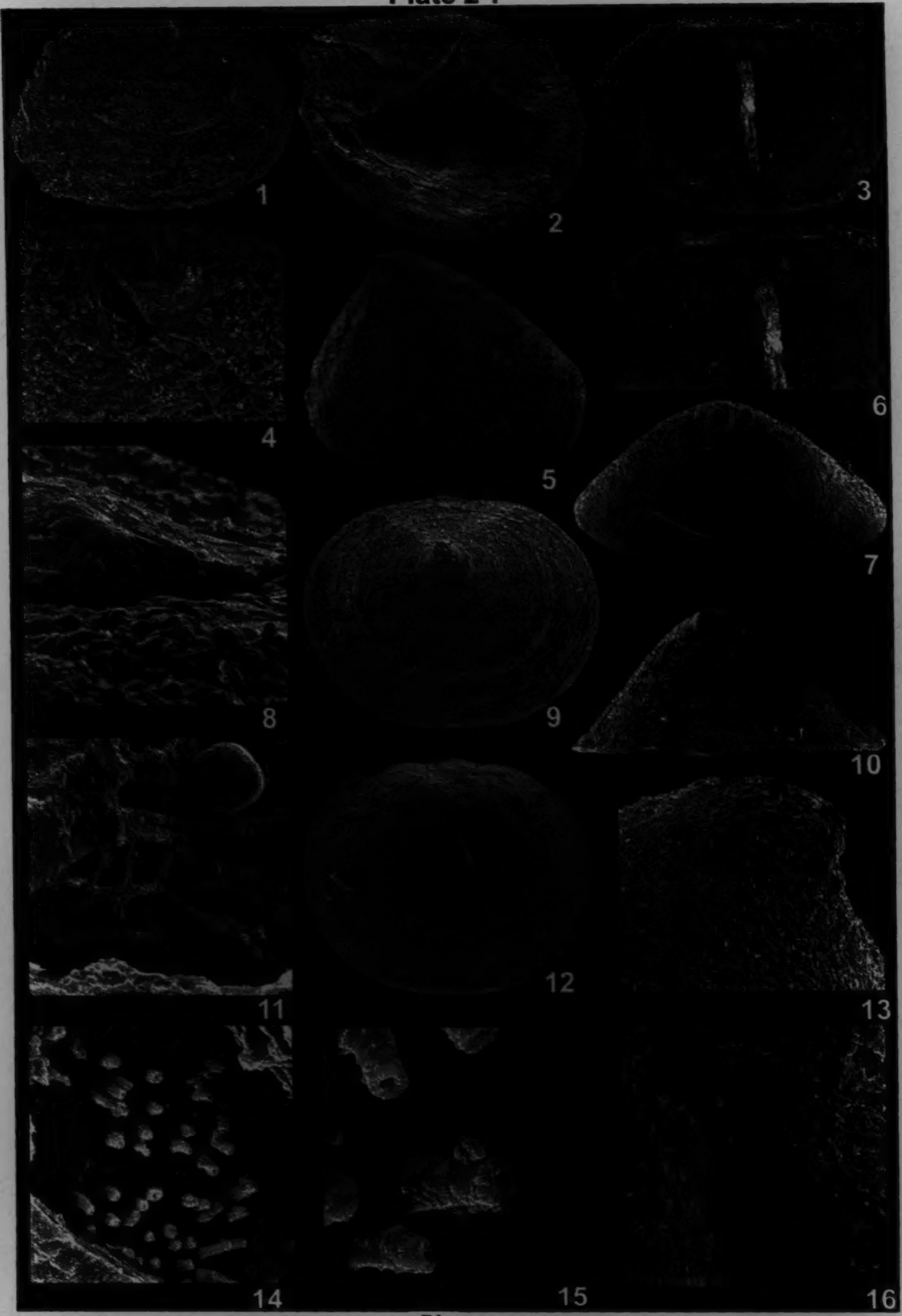
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Plate 2-8 *Tasbulakia ondata* new species from the Middle Ordovician (Llanvirn) near Ponon Trehue (PT-1)

1. External view of brachial valve; CEGH-UNC 19608; x47.
2. Oblique lateral view of brachial valve; CEGH-UNC 19609; x42.
3. Interior of brachial valve; CEGH-UNC 19610; x29.
4. Oblique lateral view of small brachial valve; CEGH-UNC 19611; x49.
5. Internal view of large pedicle valve; CEGH-UNC 19612; x26.
6. Oblique lateral view of large brachial valve; CEGH-UNC 19613; x30.
7. Secondary shell structure of the apical process in 9; CEGH-UNC 19614; x270.
8. Close up of a single larval pit in 1; CEGH-UNC 19608; x11500.
9. Internal view of broken pedicle valve; CEGH-UNC 19614; x 28.
10. Inferior view of 9; CEGH-UNC 19614; x26.
11. Close up of pillars in 7; CEGH-UNC 19614; x767.
12. Close up of laminae in 7; CEGH-UNC 19614; x767.
13. Close up of broken apical process in 9; CEGH-UNC 19614; x92.
14. Muscle scar in 9, represented as a depression; CEGH-UNC 19614; x127.
15. Close up of 14, showing cellular structures; CEGH-UNC 19614; x920.
16. Oblique superior view of median septum in 3; CEGH-UNC 19610; x51.

Plate 2-8

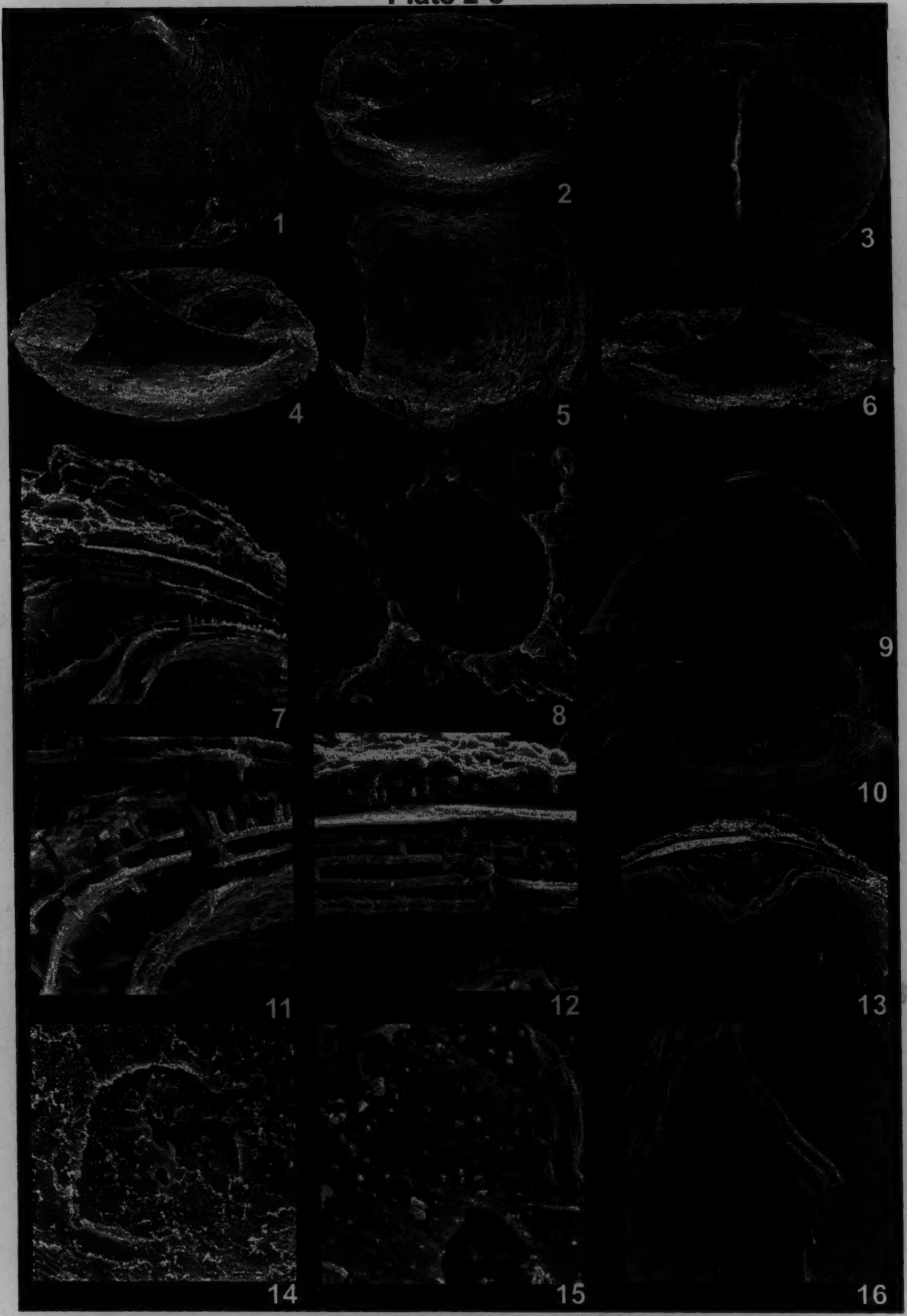

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Plate 2-9 *Eoconulus talathus* new species from Lower Ordovician (Arenig) strata of the Gualcamayo Formation (RG0-7).

1. External view of brachial valve; CEGH-UNC 19615; x69.
2. Lateral view of 1; CEGH-UNC 19615; x62.

Eoconulus talathus new species from Middle Ordovician (Llanvirn) strata of the Las Aguaditas Formation (LA 0-10cm).

3. External view of brachial valve; CEGH-UNC 19616; x66.
4. Internal view of brachial valve; CEGH-UNC 19617; x65.
5. Internal view of 3; CEGH-UNC 19616; x69.
6. Lateral view of 4; CEGH-UNC 19617; x64.
7. Close up of rod-like septum in 5; CEGH-UNC 19616; x256.
8. Lateral view of 3; CEGH-UNC 19616; x65.
9. External view of brachial valve with complete apex; CEGH-UNC 19617; x64.
10. Lateral view of exfoliated area of larval valve in 13; CEGH-UNC 19618; x920.
11. Close up of larval valve in 3; CEGH-UNC 19616; x164.
12. Close up of complete larval valve in 9; CEGH-UNC 19617; x219.
13. Close up of larval valve; CEGH-UNC 19618; x184.
14. Superior view of pitting in 10; CEGH-UNC 19618; x920.
15. Larval pitting of 11 showing two sizes; CEGH-UNC 19616; x1150.

Plate 2-9

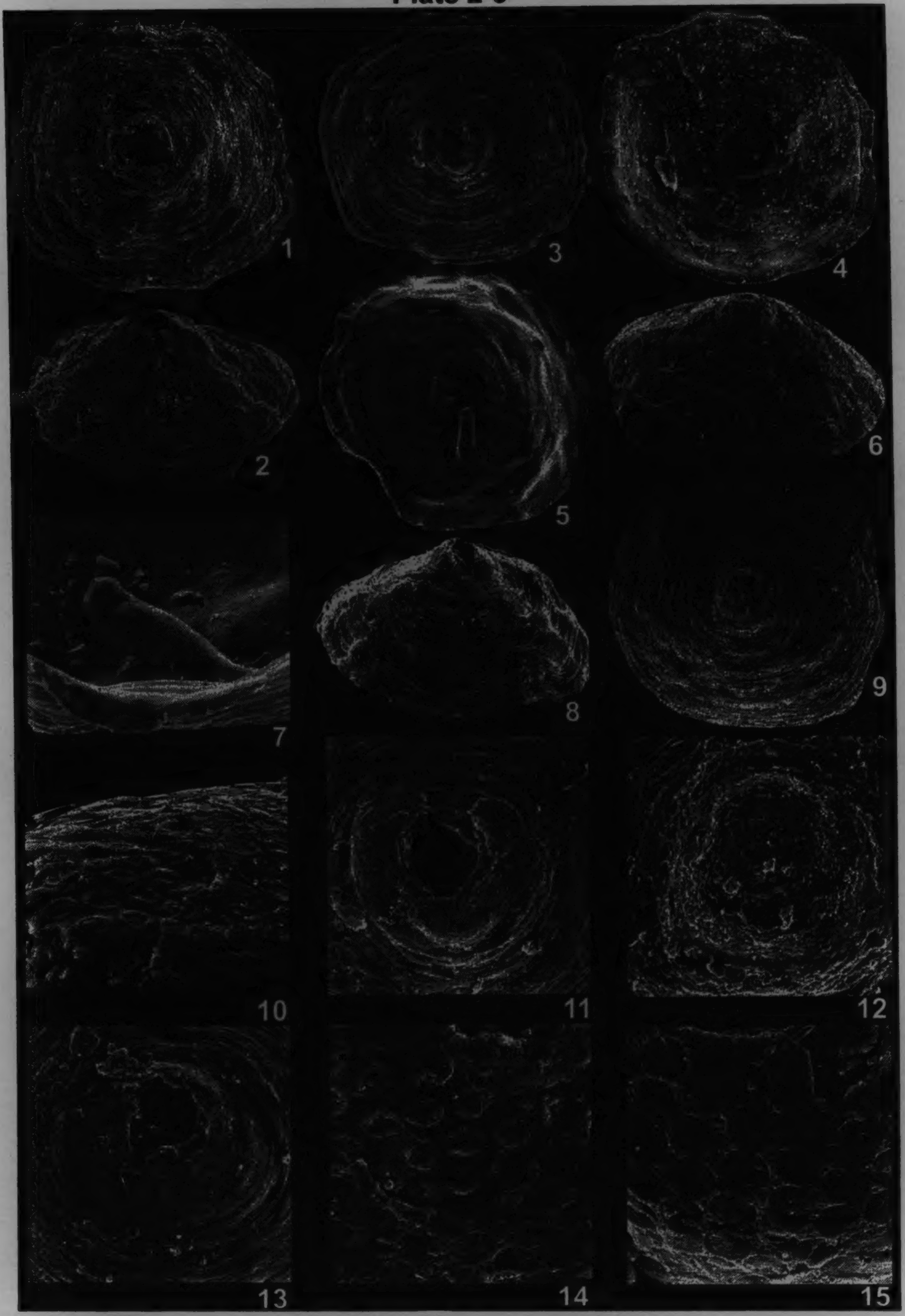
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Plate 2-10 *Undiferina viracocha* new species from Lower Ordovician (Arenig) strata of the Gualcamayo Formation (RG0-7).

1. Internal view of brachial valve; CEGH-UNC 19619; x21.
2. Oblique lateral view of broken brachial valve; CEGH-UNC 19620; x28.
3. Oblique lateral view of brachial valve in 1; CEGH-UNC 19619; x27.
4. External view of pedicle valve; CEGH-UNC 19621; x23.
5. Internal view of broken brachial valve in 2; CEGH-UNC 19620; x23.
6. Internal view of brachial valve; CEGH-UNC 19622; x23.
7. Internal view of pedicle valve; CEGH-UNC 19623; x23.
8. Anterior view of broken brachial valve in 2; CEGH-UNC 19620; x34.
9. Close up of larval valve in 6; CEGH-UNC 19622; x 115.
10. Oblique posterior view of pedicle valve in 4; CEGH-UNC 19621; x25.
11. Close up of larval valve in 4; CEGH-UNC 19621; x137.
12. Close up of median buttress in 8; CEGH-UNC 19620; x87.
13. Close up of cellular structure in 1; CEGH-UNC 19619; x206.
14. Close up of larval pitting in 6; CEGH-UNC 19622; x1586.
15. Close up anterocentral muscle scar in 5; CEGH-UNC 19620; x307.
16. Close up of cardinal muscle scar in 5; CEGH-UNC 19620; x82.

Plate 2-10

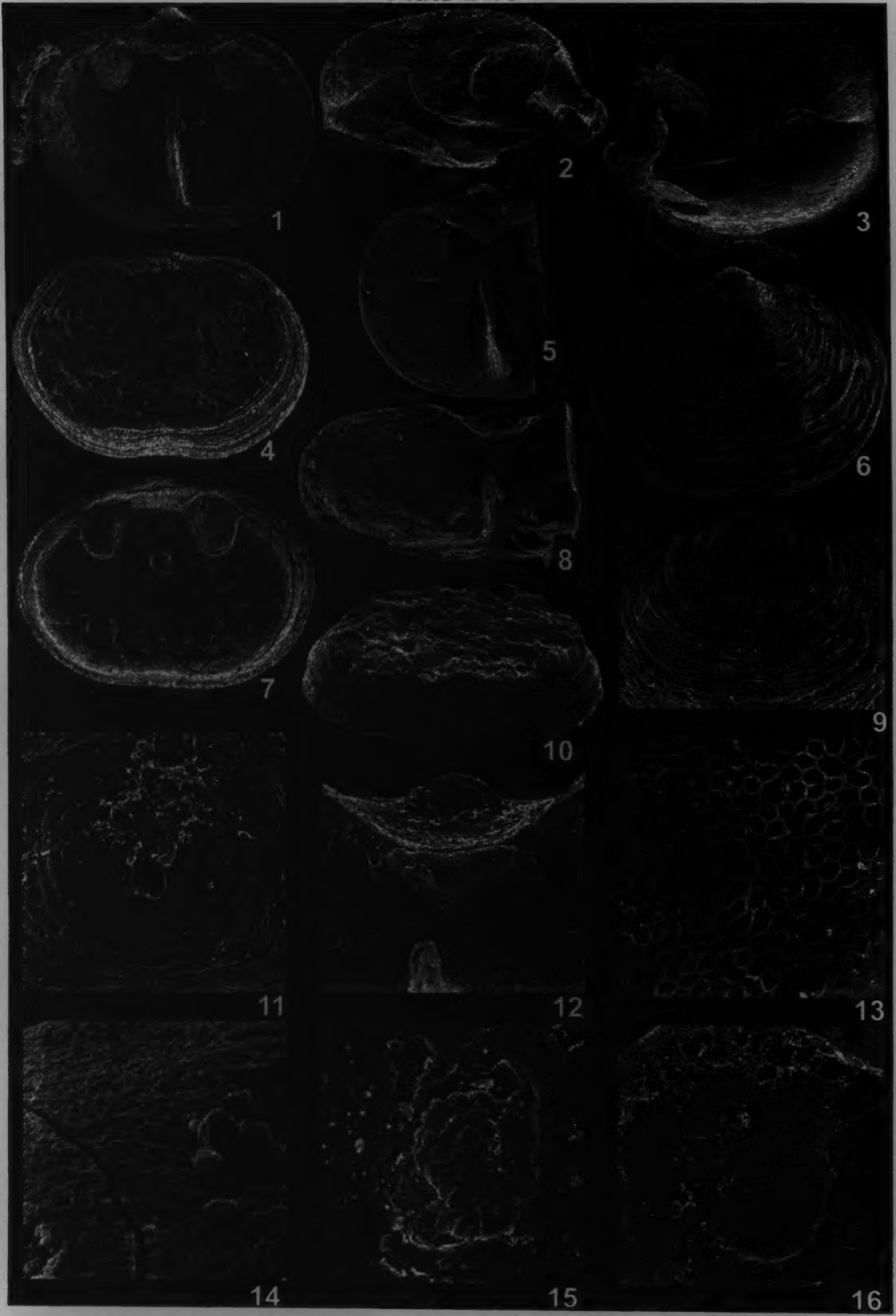
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Plate 2-11 *Scaphelasma naithum* new species from Lower Ordovician (Arenig) strata of the Gualcamayo Formation (RG0-7).

1. External view of brachial valve; CEGH-UNC 19622; x50.
2. Oblique lateral view of brachial valve; CEGH-UNC 19623; x58.
3. Internal view of brachial valve in 2; CEGH-UNC 19623; x47.
4. External view of pedicle valve; CEGH-UNC 19624; x58.
7. Internal view of pedicle valve; CEGH-UNC 19625; x57.
10. Close up of larval valve in 1; CEGH-UNC 19622; x160.
11. Close up of secondary shell structure in 2; CEGH-UNC 19623; x320.
13. Close up of larval valve in 4; CEGH-UNC 19624; x171.
14. Close up of larval pitting in 13; CEGH-UNC 19624; x1200.

Scaphelasma naithum new species from Middle Ordovician (Llanvirn) strata of the Las Aguaditas Formation (LA 0-10cm).

5. External view of broken brachial valve; CEGH-UNC 19626; x81.

Scaphelasma naithum new species from the Middle Ordovician (Llanvirn) near Ponon Trehue (PT-1).

6. Internal view of pedicle valve, showing apical process; CEGH-UNC 19627; x60.
8. Internal view of brachial valve; CEGH-UNC 19628; x56.
9. Lateral view of brachial valve in 8; CEGH-UNC 19628; x69.
12. Close up of apical process in 6; CEGH-UNC 19627; x96.
15. Close up of pillars on delaminated interior of brachial valve in 8; CEGH-UNC 19628; x400.

Plate 2-11

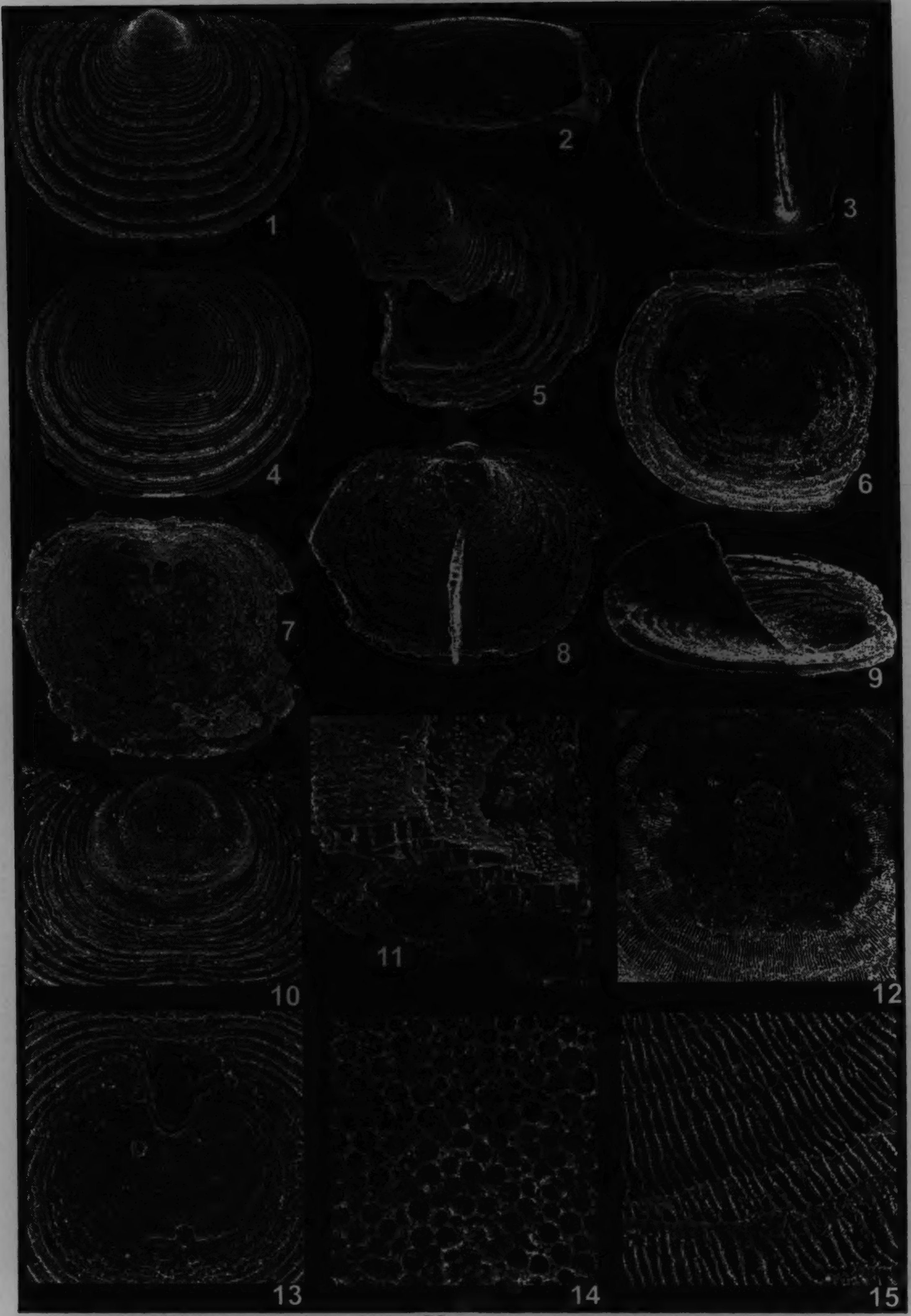
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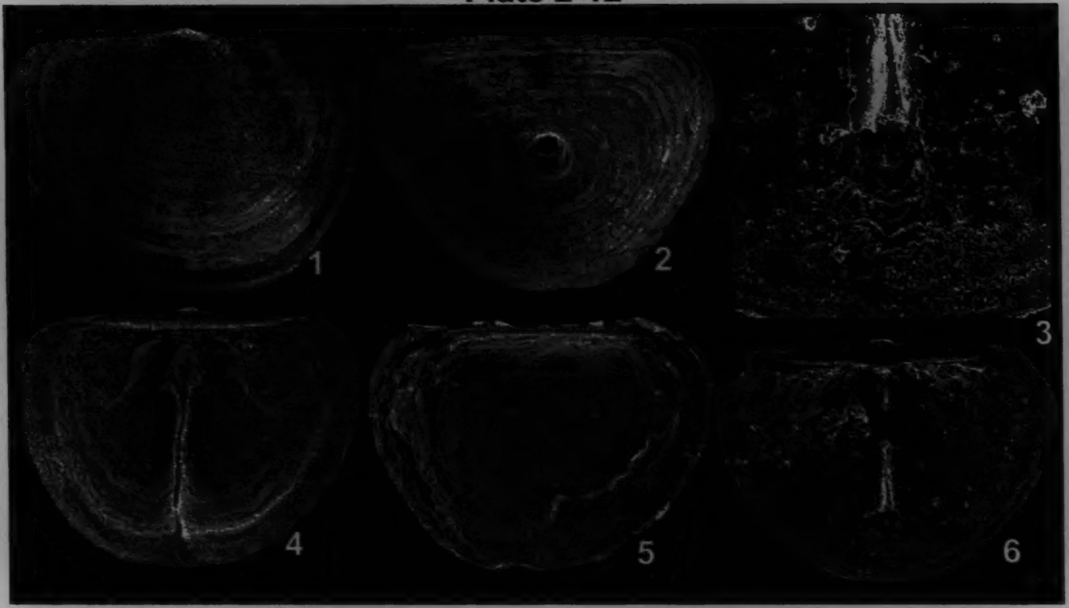
Plate 2-12 *Torynelasma suecicum* Holmer from Lower Ordovician (Arenig) strata of the Gualcamayo Formation (RG0-7).

1. External view of brachial valve; CEGH-UNC 19629; x25.
2. External view of pedicle valve; CEGH-UNC 19630; x42.
3. Close up of broken median septum in 6; CEGH-UNC 19631; x115.
4. Internal view of brachial valve in 1; CEGH-UNC 19629; x23.
5. Internal view of pedicle valve in 2; CEGH-UNC 19630; x42.
6. Internal view of pedicle valve; CEGH-UNC 19631; x41.

Plate 2-12



CHAPTER 3

Acrotretids from the Silurian of North America

INTRODUCTION

The Order Acrotretida, a taxon that has a worldwide distribution and a range from the Cambrian to the Devonian, is generally poorly represented in rocks of Silurian age. This is true for the Silurian strata of North America, as prior to this work, only three monospecific genera had been described from them. They are: *Artiotreta parva* and *Acrotretella siluriana* from the Lower Silurian (Wenlock) of Oklahoma (Ireland, 1961), Missouri, and Illinois (Satterfield and Thompson, 1969), and *Opsiconidion* sp. from the middle Silurian of Ontario (von Bitter and Ludvigsen, 1979). In rock samples initially collected for trilobites or conodonts from northern Canada and Oklahoma, respectively, new species of each of these three genera have been isolated. Thus, this study will substantially increase our knowledge of the diversity of acrotretids in the Silurian of North America.

LOCALITIES AND BIOGEOGRAPHY

Oklahoma

The specimens described are from conodont localities in south central Oklahoma near the Arbuckle Mountains (Fig. 3-1) and were collected by J.E. Barrick. Detailed stratigraphic information can be found in Barrick and Klapper (1976 and 1992).

Section C1-3 from the Fitzhugh Member of the lower Clarita Formation is a Lower Silurian (Wenlock) grey-weathering, fossiliferous limestone containing conodonts

(Barrick and Klapper, 1976; Barrick, 1977), trilobites (Holloway, 1980; Emielity, 1989), and rhynchonelliform (Amsden, 1968) and linguliform (Ireland, 1961) brachiopods. This unit would have been located deep on a shelf bordering the Tethys Sea during the Wenlock (Fig. 3-2). *Artiotreta parva* was the only species isolated from the present samples, which were collected from near the type locality for this species. It was surprising that no specimens of *Acrotretella siluriana* were recovered, as these two species seem to share an association (Ireland, 1961; Satterfield and Thompson, 1969).

Section PR-3 is an Upper Silurian (Pridoli) argillaceous wackestone and mudstone in the uppermost Henryhouse Formation. Previous studies on this area have described trilobites (Campbell, 1967; Adrain, 1996), sponges (Finks, 1995), crinoids (Strimple, 1975, 1981; Frest and Strimple, 1981), corals (Sutherland, 1965), conodonts (Barrick and Klapper, 1992), and articulated brachiopods (Boucot and Amsden, 1958; Amsden, 1951, 1969). The species *Opsiconidion aldridgei* Cocks was recovered from this locality, which marks its first occurrence in North America. It has been previously described from the Llandovery of the Welsh Borderlands, Austria, and Estonia, and the Lower Devonian of Australia.

Arctic Islands

All material was collected by B.D.E. Chatterton. Previous studies on the Cape Phillips Formation of Cornwallis Island include recoveries of radiolarians (Goodbody, 1982; Lenz, 1986), conodonts (Jowett and Barnes, 1999), graptolites (Lenz and Melchin, 1990, 1991; Lukasik and Melchin, 1997), sponges (Rigby and Chatterton, 1989), trilobites (Perry and Chatterton, 1977; Adrain and Edgecombe, 1997), articulated brachiopods (Ning, 1989), and microvertebrate remains (Barrow *et al.*, 1999). Inarticulated brachiopods from this area have not yet been described, however, and those present here were collected from two localities within the Lower Silurian (Wenlock) of the Cape Phillips Formation near Abbott River on Cornwallis Island (CAR-1 and CAR-80) (Fig. 3-1). Detailed stratigraphic information on these localities can be found in Perry and Chatterton (1977) and Rigby and Chatterton (1989). Both localities contain the new species *Opsiconidion bohunensis* and *Acrotretella stepplella*, but *Artiotreta sammera* was isolated from CAR-1 only.

Northwest Territories

All material was collected by B.D.E. Chatterton. A single new species, *Opsiconidion emmotus*, was identified from Lower Silurian (Llandovery) strata (AV 2 11.5) from the limestones of the Whittaker Formation in the Avalanche Lake area of the Mackenzie Mountains, southwestern District of Mackenzie, Northwest Territories, Canada (Fig 3-1). Detailed stratigraphic information can be found in Chatterton and Perry (1983) and Over and Chatterton (1987). Previous studies in the Avalanche Lake area have included thelodonts (Soehn *et al.*, 2001), sponges (Rigby and Chatterton, 1994; 1999), ostracods (Copeland, 1978), conodonts (Over and Chatterton, 1987), trilobites (Chatterton and Perry, 1983, 1984; Edgecombe, Speyer, and Chatterton, 1988; Siveter and Chatterton, 1996), and articulated brachiopods (Jin and Chatterton, 1997). This locality was in the Paleo Tethys Ocean during the Landovery.

SYSTEMATIC PALEONTOLOGY

Subphylum LINGULIFORMEA Williams *et al.*, 1996
Class LINGULATA Gorjanskij and Popov, 1985
Order ACROTRETIDA Kuhn, 1949
Superfamily ACROTRETOIDEA Schuchert, 1893

Family BIERNATIDAE Holmer, 1989

DIAGNOSIS: "Shell with narrow, convex posterior margin; ventral valve narrow, highly conical; ventral pseudointerarea strongly apsacline, poorly defined laterally; intertrough poorly developed or absent; dorsal pseudointerarea small, divided; apical process absent; dorsal interior with high triangular median septum bearing dorsally convex surmounting plate or rod on posterior slope; anterior slope of septum undercut; dorsal anterocentral scars absent" (Holmer and Popov, 2000: 130). *Ordovician (upper Tremadoc)-Middle Devonian, ?Upper Devonian.*

REMARKS: As with the specimens of *Opsiconidion* described by Brock *et al.* (1995) from Australia, all of the specimens figured here (Plate 3-1, Figs. 1-12) possess anterocentral muscle scars lateral to the median septum.

Genus OPSICONIDION Ludvigsen, 1974

SYNONYMY: *Caenotreta* Cocks, 1979

TYPE SPECIES: *Opsiconidion arcticon* Ludvigsen, 1974, from the Lower Devonian Michelle Formation, Yukon Territory.

DIAGNOSIS: "Minute torynelasmatids with a nearly circular, flat brachial valve which has a very shallow, anteriorly widening furrow. The pedicle valve is highly conical and bears a well-defined pedicle opening at the apex. The dorsal interior is dominated by a triangular, blade-like median septum flanked by a pair of cardinal scars. The dorsal protegulum is large and prominent and carries a U-shaped lateral swelling. The ventral protegulum is similarly large, conical, and has a foramen at its apex. Pedicle valve interiors appear to be smooth and to lack muscle scars. Fine growth lines occur on the exterior of both valves. The protegulum of both valves is ornamented by a characteristic step-like, pitted pattern of one or more size ranges" (von Bitter and Ludvigsen 1979: 706). *Lower Ordovician (Lower Llandeilo)-Middle Upper? Devonian.*

SPECIES INCLUDED: *O. arcticon* Ludvigsen, 1974, Lower Devonian of Yukon, Ontario, and Victoria and New South Wales, Australia; *O. aldridgei* Cocks, 1979, Lower Silurian (Llandovery) of Welsh Borderlands, Austria, Estonia, and Oklahoma, Upper Silurian (Pridoli) of Oklahoma, Lower Devonian of Victoria and New South Wales, Australia; *O. minor* Popov, 1981, Lower Devonian of Russia, and of Victoria and New South Wales, Australia; *O. ephemera* Mergl, 1982, Upper Silurian of Bohemia; *O. podlasiensis* Biernat, 1984, Silurian of Poland; *O. praecursor* Popov and Holmer, 1994, Upper Ordovician of Estonia; *O. robustum* Brock, Engelbretsen, and Dean-Jones, 1995, Lower Devonian of Victoria and New South Wales, Australia; *O. nudum* Sutton, Bassett, and Cherns, 2000, Lower Ordovician of Wales; *O. bohunensis* new species, Lower Silurian (Wenlock) of Cornwallis Island; *O. emmotus* new species, Lower Silurian (Wenlock) the Northwest Territories.

UNDESCRIBED SPECIES: *O.* sp. Von Bitter and Ludvigsen, 1979, Upper Ordovician and Lower Silurian of Ontario.

Opsiconidion aldridgei Cocks, 1979

Plate 3-1, Figures 1-11

MATERIAL: 70 brachial valves and 62 pedicle valves from the uppermost Henryhouse Formation (PR-3).

DIAGNOSIS: "Pedicle valve acute, high cone; pseudointerarea greatly reduced and flat; foramen at apex of cone. Larval valve large with one size of pits. Brachial valve weakly convex, subcircular in outline with the widest point at midline; median septum triangular, with two parallel rods and narrow surmounting plate; cardinal and anterocentral muscle scars visible. Brachial larval valve with U-shaped bulge opening anteriorly; single pit size with minimal cross cutting. Shell ornament simple concentric, well-defined fila" (Cocks, 1979: 96, 98).

DESCRIPTION: The shell ornamentation consists of simple concentric, well-defined growth lines (Pl. 3-1, Figs. 3 and 4). The pedicle valve is an acute, high cone (Pl. 3-1, Fig. 6) with a greatly reduced and flat pseudointerarea (Pl. 3-1, Fig. 4). The foramen is located at apex of cone. The pedicle larval valve is large with one size of pits showing minimal cross cutting (Pl. 3-1, Figs. 8, 9, 11, and 12). The brachial valve is weakly convex and subcircular in outline (Pl. 3-1, Fig. 5), with the widest point at midlength (Pl.

3-1, Figs. 1 and 3). The median septum is triangular, with two parallel rods and a narrow surmounting plate (Pl. 3-1, Figs, 1 and 5). The lamellae of the secondary shell structure can be seen in a broken septum (Pl. 3-1, Figs. 7 and 10). Both the cardinal and anterocentral muscle scars are visible as shallow depressions (Pl. 3-1, Fig. 1). The brachial larval valve has a U-shaped bulge opening anteriorly (Pl. 3-1, Figs. 2, and 3), and is ornamented by a single pit series with minimal cross cutting.

DISCUSSION: This marks the first occurrence of this species in North America and fills in part of the time gap from the Early Silurian of England (Cocks, 1979) to the Early Devonian of Australia (Brock *et al.* 1995). The Oklahoma material is very similar to that of Cocks (1979) from the Silurian (Llandovery) of the Welsh Borderland, England, except, like that of Brock *et al.* (1995) from the Devonian of Australia, the brachial valve possesses a much narrower median surmounting plate (Pl. 3-1, Fig. 1). The pits on the larval valve display more extensive cross cutting than those of Cocks (Pl. 3-1, Fig. 11). However, this is a very difficult feature to study without the aid of a SEM, and it is even more difficult to see in Cocks' figured material. The existence of cross-cutting pits is itself a vague character and may not actually be useful in species diagnosis, as it is of a functional nature and may be affected by environmental (phenetic) triggers rather than genetic ones. The medial furrow used by Cocks (1979) to distinguish between *O. aldridgei* and *O. celloni*, but determined by Brock *et al.* (1995) to be due only to intraspecies variation, is not found the Oklahoma material described here (Pl. 3-1, Fig. 1). The sizes of the Oklahoma material (brachial valve length: 0.7-0.8 mm, mean=0.75; width: 0.7-0.9 mm, mean=0.8; N=132) fall within the range of the type material (Cocks, 1979). All of the pedicle valves found in the Henryhouse Formation were broken, and only the apical tips (including the larval valve and a small portion of the adult valve) were recovered.

Opsiconidion bohunensis new species

Plate 3-2, Figures 1-16; Plate 3-3, Figures 1-6.

ETYMOLOGY: After J. E. and S. L. Bohun, the author's academic comrades.

HOLOTYPE: UA 13185, brachial valve (Pl. 3-2, Figs. 1-2).

LOCALITY AND MATERIAL: 16 brachial valves and 8 pedicle valves from the Lower Silurian (Wenlock) strata of the Cape Phillips Formation, Abbott River, Cornwallis Island (CAR-1 And CAR-80).

DIAGNOSIS: *Opsiconidion* with transversely oval shell outline at commissure; ornamentation of rounded growth lines; pedicle valve subconical, wider than high; pedicle pseudointerarea present but weakly developed, catacline to apsacline; foramen circular, apical, slightly posteriorly directed, enclosed within larval valve; brachial valve flattened to weakly convex; brachial median septum long, low, triangular, with slight rod-like swelling posterodorsally; cardinal muscle scar pair forms distinct impressions posterolaterally; anterocentral muscle scar pair less distinct, anteromedial to central muscle scars; pedicle larval valve flares basally with narrow apex; brachial larval valve weakly convex with swelling v-shaped; two series of larval pitting consisting of fine pits cross cut by distinctly larger pits.

DESCRIPTION: The adult shell of both valves is ornamented with low, rounded growth lines (Pl. 3-2, Fig. 4). The outline of the brachial valve is transversely oval (Pl. 3-2, Fig. 1, 3; Pl. 3-3, Figs. 1-2), as the length (0.74 mm) is only 67% of the width (1.1 mm; N=16). Internally, the brachial valve is dominated by a long (68% of valve length), moderately high (H:L 0.35) median septum (Pl. 3-2, Figs. 1-3, 5). Its highest point is a short distance behind the anterior end, and forms the anteroventral end of a swollen rod-like structure that passes through the septum posterodorsally (Pl. 3-2, Fig. 2). The cardinal muscle scars are suboval depressions posterolateral to the septum and the anterocentral scars are faint depressions anteromedial to the cardinal scars (Pl. 3-2; Figs. 3, 5). The brachial pseudointerarea extends for 53% of the valve width and is interrupted by a shallow median sulcus (Pl. 3-2, Figs. 1, 3, 5). The larval valve is 20% of the total valve width and has an anterior facing, U-shaped bulge (Pl. 3-2, Fig. 4). The ornament is comprised of two sets of pits (Pl. 3-2, Figs. 14-16; Pl. 3-3, Figs. 3-6); the initial set consists of fine (0.002-0.006 mm) pits interrupted, or in some cases totally obliterated, by the large (diameter: 0.01-0.06 mm), circular, flat bottomed, extensively cross cutting pits.

The pedicle valve (Pl. 3-2; Figs. 6, 12) is broadly convex, with a height to width ratio of 60% (N=8). The larval valve flares basally and has a pointed, posteriorly directed apex (Pl. 3-2, Fig. 13). The small foramen (0.11 mm) is located at the end of the apex (Pl. 3-2, Fig. 10). The pedicle pseudointerarea is catacline to apsacline and weakly developed. The secondary shell layer of both valves consists of a series of alternating lamellae and pillars (pl. 3-2, Figs. 8, 11).

DISCUSSION: The pedicle valve of *Opsiconidion bohunensis* is a much lower and more asymmetrical cone, as compared to all other species within the genus. Like *Opsiconidion robustum* from the Lower Devonian of Australia (Brock *et al*., 1995) and *Opsiconidion emmotus* from the Lower Silurian of the Northwest Territories, the apex curves posteroventrally and thus the foramen is directed more posteriorly than ventrally. The pseudointerarea is only weakly developed, but is more flattened as compared to that of other *Opsiconidion* species. The outline of the brachial valve is more transversely oval or polygonal than that of the other species, whose valves are all subcircular to circular. The larval pits show cross cutting of the large pit series, but this is less extensive than that of *O. arcticon*, *O. emmotus*, and *Opsiconidion aldridgei*, and there are a few areas where the small series of pits are still present, as in the Ordovician species *Opsiconidion praecursor* (Popov and Holmer, 1994) and *Opsiconidion nudum* (Sutton *et al*., 2000). The cardinal muscle scars are circular, as compared to oval in *O. emmotus* and *O. aldridgei*. *O. bohunensis* is placed within this genus due to the rod-like projections in the median septum and the u-shaped lateral swellings in the brachial larval valve.

Opsiconidion emmottus new species

Plate 3-4, Figures 1-6; Plate 3-5, Figures 1-14.

ETYMOLOGY: After L. C. Emmott, the author's friend and an unfaltering supporter of this work.

HOLOTYPE: UA 13194, brachial valve (Pl. 3-4, Figs. 2-3, 6).

LOCALITY AND MATERIAL: 147 brachial valves and 202 pedicle valves from the Lower Silurian (Llandovery) strata of Avalanche Lake in the Mackenzie Mountains, Northwest Territories (AV2 11.5).

DIAGNOSIS: *Opsiconidion* with highly conical pedicle valve; weak, slightly apsacline pseudointerarea, slightly recurved apex ending in an elongated tube, and posteroventrally facing foramen. Brachial valve subcircular, with V-shaped lateral swellings in larval valve; cardinal muscle scars depressed, ovate; median septum. Larval pits single series, extensively cross cut.

DESCRIPTION: The post-larval ornamentation on both valves consists of faint concentric growth lines. The secondary shell layer consists of rod-like pillars (Pl. 3-4, Fig. 13) alternating with horizontal lamellae.

The brachial valve is subcircular to ovate (Pl. 3-4, Figs. 1, 3; Pl. 3-5, Fig. 1) and shallowly convex, with a length (0.41 mm) to width (0.49 mm) ratio of 0.84 (N=147).

The brachial pseudointerarea is short (29% of the total valve width) with a slight medial sulcus (Pl. 3-4, Figs. 3, 6; Pl. 3-5, Fig. 2). The cardinal muscle scars are small and faint ovate depressions located anterolateral to the pseudointerarea (Pl. 3-4, Figs. 3, 6; Pl. 3-5, Figs. 2-3). The median septum extends for 57% of the valve length (Pl. 3-4, Fig. 3; Pl. 3-5, Fig. 1) and possesses two rod-like projections arranged at oblique angles to one another (Pl. 3-4, Fig. 2). The brachial larval valve is large (comprising 38% of the total valve width), circular and the U-shaped swelling is pointed posteriorly (Pl. 3-4, Fig. 1, 4). The larval micro-ornament consists of a single series (0.03-0.05 mm) of extensively cross cutting pits (Pl. 3-4, Fig. 12).

The pedicle valve (Pl. 3-4, Figs. 1-9) is a high, recurved cone with a height to width ratio of 1.42 (N=202). The apical region curves posteriorly (Pl. 3-4, Fig. 8) and is elongated into a tube that ends in a circular pedicle foramen 0.031 mm in diameter (Pl. 3-4, Fig. 9). The pedicle pseudointerarea is slightly flattened (Pl. 3-4, Fig. 7). The larval valve is 27% of the total valve height, and consists the pedicle tube and a flaring base with a pitting pattern similar to the brachial valve (Pl. 3-4, Figs. 10-11, 14). In the early post-larval shell, the base does not flare as much as that of the post-larval shell (Pl. 3-5, Figs. 4-5).

DISCUSSION: *Opsiconidion emmotus* is most similar to *Opsiconidion arcticon* (Ludvigsen, 1974) and *Opsiconidion aldridgei* (Cocks, 1979), as the height of the pedicle valve is at least twice its width, and the larval micro-ornament consists of a single series of extensively cross cutting pits. However, this species can be distinguished from these two taxa because the pedicle foramen points in a more posterior direction, and the apical region is elongated into a pedicle tube.

Family SCAPHELASMATIDAE Rowell, 1965

DIAGNOSIS: "Shell biconvex to concavoconvex with straight or weakly concave posterior margin; ornament of coarse, regularly spaced rugae, lamellose peripherally; ventral pseudointerarea with widely triangular intertrough; foramen not enclosed within larval shell; apical process vestigial to absent, usually forming low projection anterior to foramen; apical pits small, directly lateral to apical process; dorsal median septum triangular, bladelike, arising near midvalve and extending almost to anterior margin, or absent; dorsal anterocentral muscle scars directly lateral to septum" (Holmer and Popov, 2000: 122). *Middle Cambrian (Amgaian)-Upper Silurian.*

Genus ARTIOTRETA Ireland, 1961

TYPE SPECIES: *Artiotreta parva* Ireland, 1961 from the upper Silurian of Oklahoma.

DIAGNOSIS: Shell subcircular. Pedicle valve convex, hemispherical, with slight conical appearance. Foramen well developed, round, slightly anterior and below apex, with slight calluses around opening. External ornamentation of fine, distinct growth lines, with holoperipheral growth. Protegulum not apparent. Posterior area has obvious, but broad, shallow pseudointerarea; no intertrough; slight, distinct notch at hinge line. Growth lines continuous across pseudointerarea.

Brachial valve slightly convex; with prominent protegulum, and very fine growth lines. Interior smooth, muscle scar depressions lacking. Median septum prominent, unbranched, bladelike, beginning near center of valve and sloping upward with maximum height near anterior margin (adapted from Ireland, 1961, p. 1138). *Lower Silurian (Wenlock).*

REMARKS: There has been some suggestion that *Artiotreta* is a junior synonym of the Ordovician genus *Scaphelasma* (most recently Holmer and Popov, 2000). However, in *Artiotreta*, the pedicle foramen is fully included within the larval valve, wile it is only partially included in *Scaphelasma*, which is enough to warrant a separate genus. Ireland (1961) suggested that *Artiotreta* was derived from *Scaphelasma* and thus placed them within the same family.

SPECIES INCLUDED: *A. parva* Ireland, 1961, Lower Silurian of Oklahoma, Missouri, and Illinois; *A. sammera* new species, Lower Silurian of Cornwallis Island.

Artiotreta sammera new species

Plate 3-6, Figures 1-16

ETYMOLOGY: In memory of Samantha Duffy, the author's long-time feline companion.

HOLOTYPE: UA 13199, brachial valve (Pl. 3-6, Figs. 1, 5).

MATERIAL AND LOCALITY: 8 brachial valves and 3 pedicle valves from Lower Silurian (Wenlock) strata of the Cape Phillips Formation, Abbott River, Cornwallis Island (CAR-1 and CAR-80).

DIAGNOSIS: *Artiotreta* with rounded, subquadrate shell outline around commissure; greater width than length; maximum width near midline; ornamentation of rounded, ridge-like fila; pedicle valve asymmetrically conical with blunt apex; pedicle pseudointerarea procline; brachial valve weakly convex with bulbous larval valve at apex; brachial median septum wedge shaped, short, high, with maximum height at midlength; cardinal muscle scars large; two distinct sets of larval pits: fine set interrupted by large circular set with very little cross cutting.

DESCRIPTION: In both valves the post-larval shell is ornamented with strong concentric growth lines (Pl. 3-6, Figs. 3, 6). The width (0.88 mm) of the slightly convex brachial valve is greater than the length (0.67 mm; L:W 0.76; N=8), giving a transversely oval or subquadrate outline to the valve (Pl. 3-6, Figs. 1, 6). The umbo of the brachial valve is marked by an inflated larval valve (0.17 mm in diameter; 19% of the total shell width; Pl. 3-6, Fig.9) with a set of fine pits (0.002-0.006 mm) surrounding a set of larger, circular, non-cross cutting pits (0.015-0.06 mm; Pl. 3-6, Figs. 14-16). Internally, the pseudointerarea is strongly anacline (Pl. 3-6, Fig. 8), 68% of the valve width, and interrupted by a shallow median groove (Pl. 3-6, Figs. 5, 7). The median septum is a high, peaked wedge that extends for 48% of the valve length. The maximum height at the valve midlength, and is 75% of the septum length (Pl. 6, Figs. 7-8). The pedicle pseudointerarea is flattened and procline (Pl. 3-6, Fig. 3). The pedicle valves are poorly preserved (N=3). The shell thickens towards the margins, and is composed of a solid primary layer overlying a secondary layer of only a few series lamellae and pillars (Pl. 3-6, Figs.12-13).

DISCUSSION: The only other species within the genus is *Artiotreta parva* from the Lower Silurian of Oklahoma (Ireland, 1961), and *Artiotreta sammera* differs in the following features: 1) the median septum is a sharpened wedge with a distinct peak at the valve midline, while that of *A. parva* is rounded and reaches its maximum height anterior to the midlength of the valve and 2) the brachial valve is transversely subquadrate and has a wider pseudointerarea than that of *A. parva* which is subquadrate.

Artiotreta parva Ireland, 1961

Plate 3-7, Figures 1-15; Plate 3-8, Figures 1-9.

MATERIAL AND LOCALITY: 85 brachial valves and 70 pedicle valves from Lower Silurian (Wenlock) strata of the Lower Clarita Formation of Oklahoma.

DIAGNOSIS: Pedicle valve low, rounded cone; intertrough well developed. Internally, narrow muscle scars extend lateral from foramen. Pedicle larval valve at apex of cone; includes whole foramen; two sizes of pitting with minimal cross cutting. Brachial valve subquadrate, shallowly convex, with prominent posterior bulge of the larval valve. Large tear-drop shaped cardinal muscle scars, lateral to small anterocentral muscle scars. Median septum rounded and wedge shaped. Shell ornament concentric, very well developed fila (modified from Ireland, 1961).

DISCUSSION: *Artiotreta parva* is the only species that has been assigned to this genus until this work. The material included in this paper is very similar to the type material, isolated from residues from the Chimney Hill Limestone, 50km away. The dimensions of the Clarita material (length: 0.4-0.5 mm, mean=0.45; width: 0.45-0.5 mm, mean=0.47; N=155; pedicle valve height: 0.15-0.2, mean=0.19) fall within the range of the type material as described by Ireland (1961). Possible later ontogenetic stages were recovered, and show thickening of the median septum and all shell margins (Pl. 3-8, Figs. 1-6).

Satterfield and Thompson (1969) reported an ecological correlation between the basal Bainbridge Formation of southeastern Missouri and southwestern Illinois and the Clarita Formation of Oklahoma, and the appearance of *A. parva* in this study supports that correlation. In both Ireland (1961) and Satterfield and Thompson (1969), *A. parva* occurs with *Acrotretella siluriana* Ireland; however, no specimens of the latter were recovered from the residues in this study.

Family TORYNELASMATIDAE Rowell, 1965

DIAGNOSIS: "Shell with wide, straight posterior margin; pedicle valve subpyramidal; pedicle pseudointerarea flat, procline to apsacline, undivided; foramen enclosed within larval shell; dorsal pseudointerarea wide, poorly divided; pedicle interior with low, ridge-like apical process supporting pedicle tube; dorsal valve with high, triangular median septum, commonly with variably developed surmounting platform; broad median buttress elevated above median groove, dorsal anterocentral scars absent" (Holmer and Popov, 2000). *Ordovician (Arenig)-Devonian.*

Genus ACROTRETELLA Ireland, 1961

TYPE SPECIES: *Acrotretella siluriana* Ireland, 1961, from the Upper Silurian of Oklahoma.

DIAGNOSIS: "Ventral valve wide, conical; ventral pseudointerarea procline to catacline; apical process and internal pedicle tube absent; dorsal pseudointerarea undivided; dorsal median septum low to high with dorsally concave surmounting platform; dorsal larval shell bulbous" (Holmer and Popov, 2000:124). *Ordovician (Caradoc)-Devonian (Lochkovian).*

SPECIES INCLUDED: *A. siluriana* Ireland, 1961, Lower Silurian (Wenlock) of Oklahoma, Missouri, and Illinois, and possibly of England; *A. tenuis* Bogolopova, 1998, Upper Ordovician of the Carnic Alps, Austria; *A. golapiensis* Biernat, 1999, Lower Ordovician of northeast Poland; *A. triseptata* Mergl, 2000, Lower Devonian (Lochkovian) of Bohemia; *A. stepplella* new species, Lower Silurian (Wenlock) of Cornwallis Island.

UNDESCRIBED SPECIES: *A.* sp. Popov, 2000, Upper Ordovician of north-central Kazakhstan.

Acrotretella stepplella new species

Plate 3-9, Figures 1-15

ETYMOLOGY: After T. M. Stepple, the author's most enthusiastic advocate.

HOLOTYPE: UA 13218, brachial valve (Pl. 3-9, Figs. 6, 9, 12, 15).

LOCALITY AND MATERIAL: 7 brachial valves and 4 pedicle valves from Silurian strata along the Abbott River, Locality 1, Cornwallis Island (CAR-1 and CAR-80).

DIAGNOSIS: *Acrotretella* with valves wider than long; pedicle valve asymmetrically conical, wider than high, with procline pseudointerarea; pedicle interior lacking apical process; foramen subcircular, apical, enclosed within larval valve; brachial valve flattened with bulbous larval valve; brachial interior with three septa: thin median septum with posterior half covered by posteroventrally concave surmounting plate and two lateral septa extending anterolaterally at 45° angles to midline; cardinal muscle scars shallow, almost indistinct, lateral to median septum; larval valves with single cross cutting series of fine pits (mean=0.0133 mm); adult prospon with weakly developed growth lines and fine perforations alternating with strong fila; shell structure consisting of lamellae separated by honeycomb structure or fine rod-like pillars.

DESCRIPTION: External microsculpture on the post-larval prosopon consists of distinct fila, weak growth lines and fine perforations (Pl. 3-9, Figs. 1, 6, 12, 15). The brachial valve is weakly convex to almost flat and hemicircular in outline with a straight posterior margin (Pl. 3-9, Figs. 6, 9). Its length (0.79 mm) is 60% of the width (1.33 mm; N=7). The larval valve is a round bulge (0.17 mm diameter) at the apex of the valve, roughly 13% of the total shell width (Pl. 3-9, Fig 3). Internally, the pseudointerarea is anacline and extends for 56% of the valve width (Pl. 3-9, Fig. 9). The median septum is a narrow rod extending 67% of the valve length (Pl. 3-9, Fig. 9). It is covered posteriorly by a broad (0.14 mm wide) and weakly concave surmounting plate, and flanked by two short (53% of the median septum length), lateral septa lying at a 45° angles.

The pedicle valve is a blunt asymmetrical cone with a flat, procline pseudointerarea (Pl. 3-9, Figs 1, 2, 7). The subcircular foramen (0.028 mm in diameter) is apical and slightly anteroventrally directed (Pl. 3-9, Figs. 2, 5). The larval shell is 13% of the total valve width (Pl. 3-9, Fig 1), and marked by a single series of small (mean=0.0133 mm), extensively cross cutting pits (Pl. 3-9, Figs. 13-14). The shell structure consists of a secondary layer with extensive lamellae (Pl. 3-9, Figs. 8, 10) separated by a vertical honeycomb structure or pillars (Pl. 3-9, Fig. 10).

DISCUSSION: *Acrotretella stepplella* has a much flatter and wider posterior margin than all other species within this genus. The morphology of the median septum in *A. stepplella* is most similar to that of *Acrotretella golapiensis* from the Arenig of Poland (Biernat and Harper, 1999), but the septa of *A. stepplella* are much shorter and narrower, and the surmounting plate is less concave.

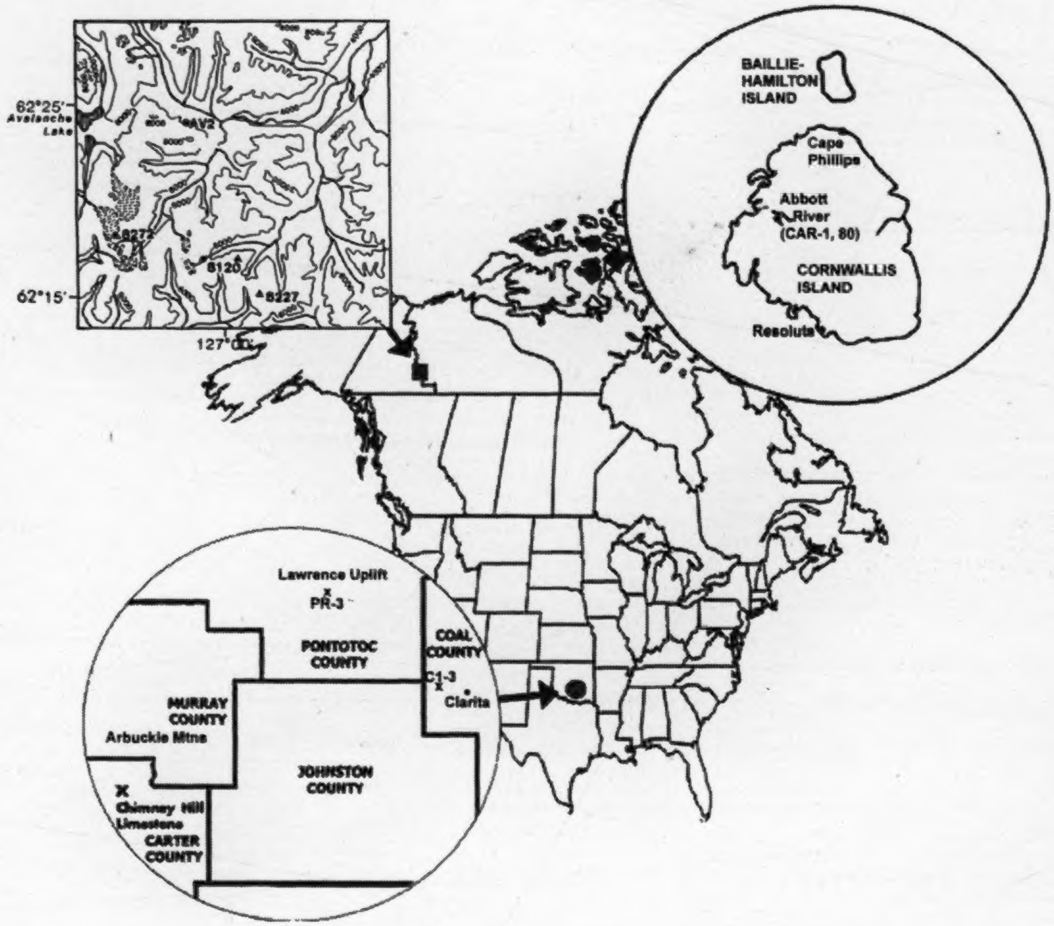

62°25'
Avalanche Lake
AV2
8272
8120
8227
62°15'
127°00'
BAILLIE-HAMILTON ISLAND
Cape Phillips
Abbott River (CAR-1, 80)
CORNWALLIS ISLAND
Resolute
Lawrence Uplift
PR-3
PONTOTOC COUNTY
COAL COUNTY
C1-3
Clarita
MURRAY COUNTY
Arbuckle Mtns
JOHNSTON COUNTY
Chimney Hill Limestone
CARTER COUNTY

Figure 3-1: Map of the North American localities. (modified from Chatterton and Perry, 1983; Over and Chatterton, 1987; and Barrick and Klapper, 1976)

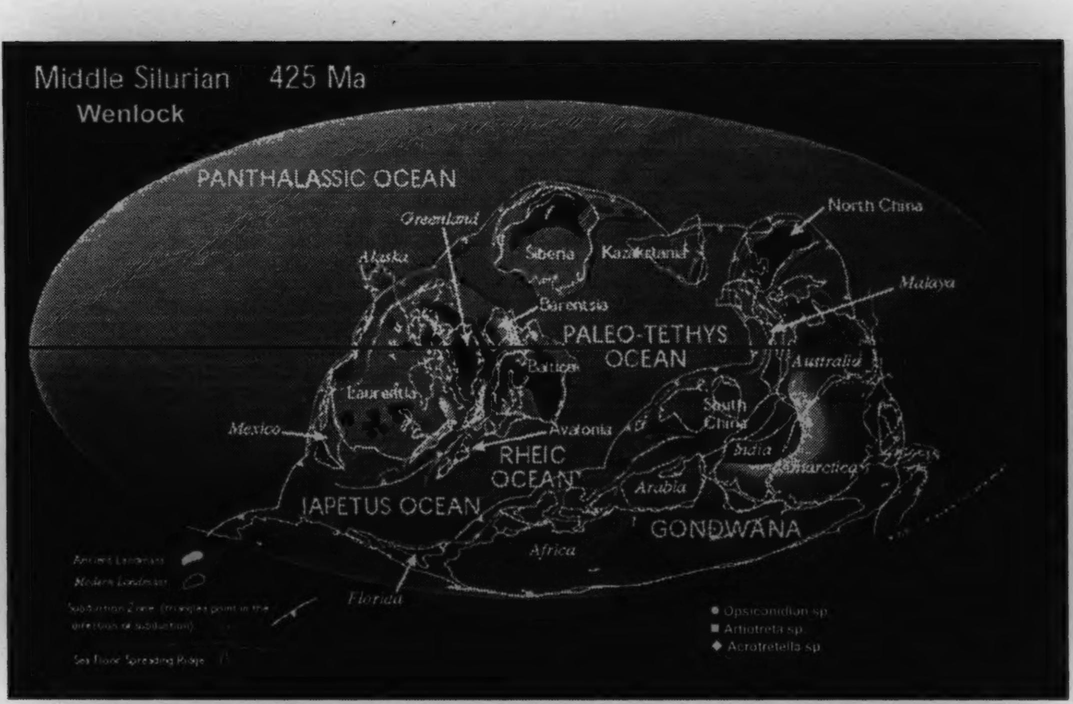

Middle Silurian 425 Ma
Wenlock
PANTHALASSIC OCEAN
Greenland
Alaska
Siberia
Kazakstania
North China
Malaya
Barentsia
PALEO-TETHYS OCEAN
Baltica
Australia
Laurentia
South China
Mexico
Avalonia
RHEIC OCEAN
India
Antarctica
Arabia
IAPETUS OCEAN
GONDWANA
Africa
Florida
Ancient Landmass
Modern Landmass
Subduction Zone (triangles point in the direction of subduction)
Sea Floor Spreading Ridge
● Opsiconidian sp.
■ Artiotreta sp.
◆ Acrotretella sp.

Figure 3-2: Acrotretid genera of the Silurian of North America. (modified from Scotese, 2000)

	Opsiconidion aldridgei	*Opsiconidion bohunensis*	*Opsiconidion emmottus*	*Artiotreta parva*	*Artiotreta sammera*	*Acrotretella stepplella*
Length	0.63	0.74	0.41	0.42	0.67	0.79
Width	0.69	1.1	0.49	0.6	0.88	1.33
Height	-	0.68	0.7	0.3	0.42	0.8
L:W	0.91	0.67	0.84	0.7	0.76	0.6
H:W	-	60	142	50	48	60
Septum % of L	79	68	57	49	42	67
Septum H:L	0.43	0.4	-	0.6	0.75	
Foramen	0.034	0.011	0.031	0.027	-	0.028
Pia % of W	40	55	29	30	68	56
Larval % of W	25	20	33	33	19	13
Pit Diameter-large	0.035-0.06	0.011-0.059	0.031-0.051	0.03-0.05	0.01-0.05	0.01-0.03
small		0.002-0.006			0.007	

Table 3-1: Measurements of the acrotretids from North America. All measurements in mm. Pia=pseudointerarea.

Plate 3-1 *Opsiconidion aldridgei* Cocks from Pridoli strata of the Henryhouse Formation, Oklahoma (PR-3).

1. Interior of brachial valve; UA 13179; x99.
2. Close up of brachial larval valve in 3; UA 13180; x226.
3. Exterior of brachial valve; UA 13180; x101.
4. Lateral view of broken pedicle valve; UA 13181; x189.
5. Oblique lateral view of brachial valve in 1; UA 13179; x102.
6. Oblique ventral view of incomplete pedicle valve; UA 13182; x200.
7. Oblique lateral view of brachial valve; UA 13183; x98.
8. Detail of broken median septum; UA 13184; x1100.
9. Close up of larval pitting in 4; UA 13181; x1998.
10. Close up of larval shell margin in 4; UA 13181; x1758.
11. Detail of broken septum in 8 showing the laminated structure of the secondary shell layer; UA 13184; x2500.
12. Close up of larval pitting in 3; UA 13180; x2153.
13. Close up of larval pitting in 6; UA 13182; x3600.

Plate 3-1

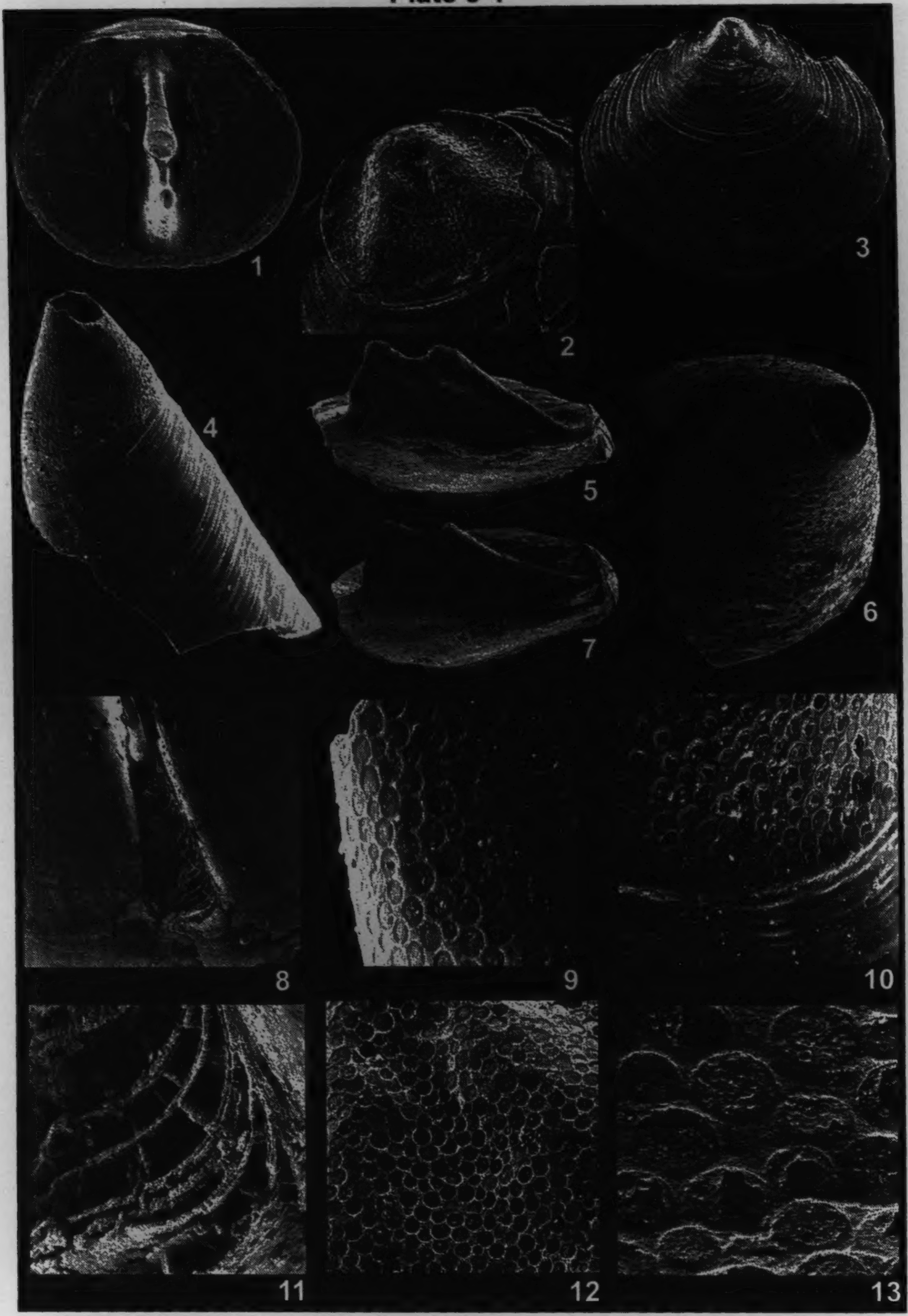

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Plate 3-2 *Opsiconidion bohunensis* new species from Wenlock strata of the Cape Phillips Formation, Abbott River, Cornwallis Island (CAR-1, CAR-80).

1. Internal view of brachial valve; UA 13185; x50.
2. Lateral view of brachial valve in 1; UA 13185; x60.
3. Internal view of brachial valve; UA 13186; x82.
4. Close up of brachial larval valve; UA 13187; x128.
5. Oblique lateral view of brachial valve in 3; UA 13186; x117.
6. External anterior view of pedicle valve; UA 13188; x120.
7. External ventral view of pedicle valve in 6; UA 13188; x128.
8. Section of broken pedicle valve in 9 showing lamellae and pillars of secondary shell layer; UA 13189; x1040.
9. Fragment of pedicle valve; UA 13189; x77.
10. Close up of pedicle foramen and surrounding larval shell from 13; UA 13190; x1760.
11. Section of broken pedicle valve in 12 showing thick primary layer and lamellae of secondary layer separated by narrow porous layers with pillars; UA 13191; x690.
12. Lateral view of broken pedicle valve; UA 13191; x110.
13. Ventral view of broken pedicle valve; UA 13190; x211.
14. Close up of pitting on the brachial larval valve in 4; UA 13187; 1483.
15. Brachial larval pitting in 4, showing cross cutting, and two size sets; UA 13187; x3179.
16. Close up of brachial larval pitting showing an area where most of the fine pits have been obliterated; UA 13192; x1534.

Plate 3-2

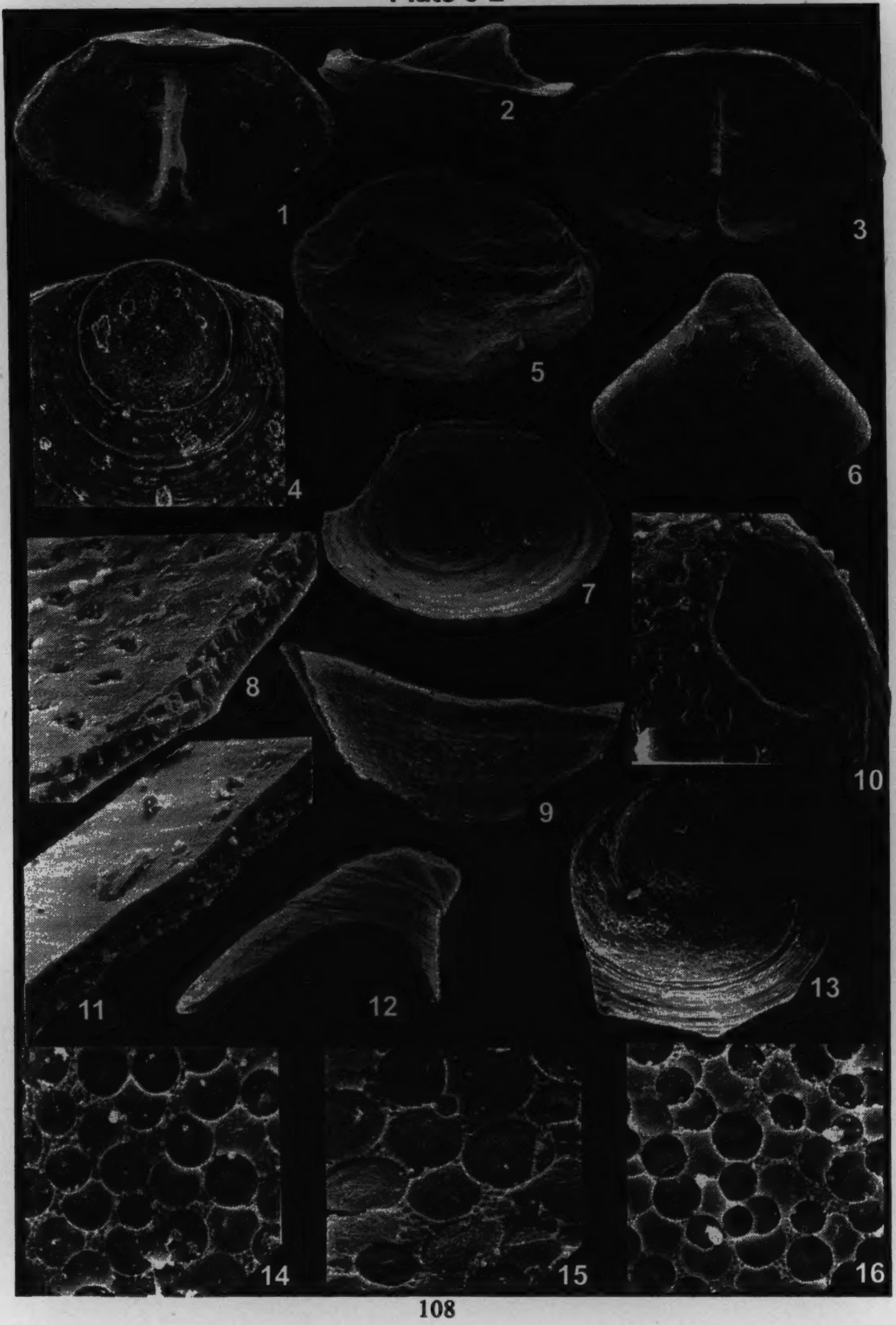
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Plate 3-3 *Opsiconidion bohunensis* new species from Wenlock strata of the Cape Phillips Formation, Abbott River, Cornwallis Island (CAR-1, CAR-80).

1. External view of brachial valve; UA 13187; x360.
2. External view of brachial valve; UA 13192; x118.
3. Close up of pitting on the brachial larval valve in 1; UA 13187; x3708.
4. Close up of brachial larval valve margin showing distinct transition from pits to growth lines; UA 13192; x1257.
5. Close up of pedicle larval valve pitting showing convex outward nature of lamella under a resorption pit; UA 13192; x3140.
6. Larval pitting from 1 showing cross cutting, and two size sets; UA 13187; x6000.

Plate 3-3

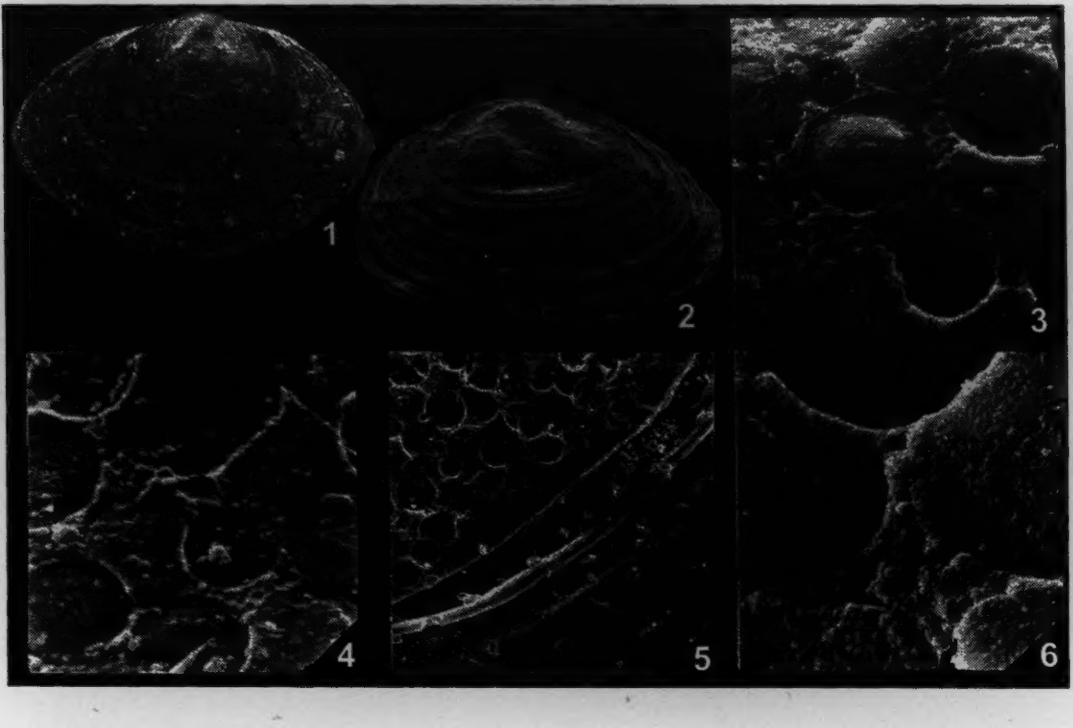

Plate 3-4 *Opsiconidion emmotus* new species from Wenlock strata, Avalanche Lake in the Mackenzie Mountains, Northwest Territories (AV2 11.5).

1. External view of brachial valve; UA 13193; x112.
2. Oblique lateral view of brachial valve in 3; UA 13194; x113.
3. Internal view of brachial valve; UA 13194; x112.
4. Close up of larval valve in 1; UA 13193; x200.
5. Internal view of pedicle valve in 9; UA 13196; x114.
6. Close up of posterior part of brachial valve in 3; UA 13194; x198.
7. Lateral view of ephebic pedicle valve; UA 13195; x117.
8. Close up of pedicle larval valve in 7; UA 13195; x201.
9. Posterior view of pedicle valve; UA 13196; x102.
10. Close up of pitting on the pedicle larval valve in 7 showing a single pit cutting through two others; UA 13195; x3294.
11. Another view of the pits in 10; UA 13195; x1678.
12. Close up of pitting on the brachial larval valve in 1 showing cross cutting; UA 13193; x2133.
13. Close up of pillar-like rods of secondary shell layer exposed in the muscle scar in 7; UA 13195; x2764.
14. Close up of pitting on pedicle larval valve in 7; UA 13195; x2138.

Plate 3-4

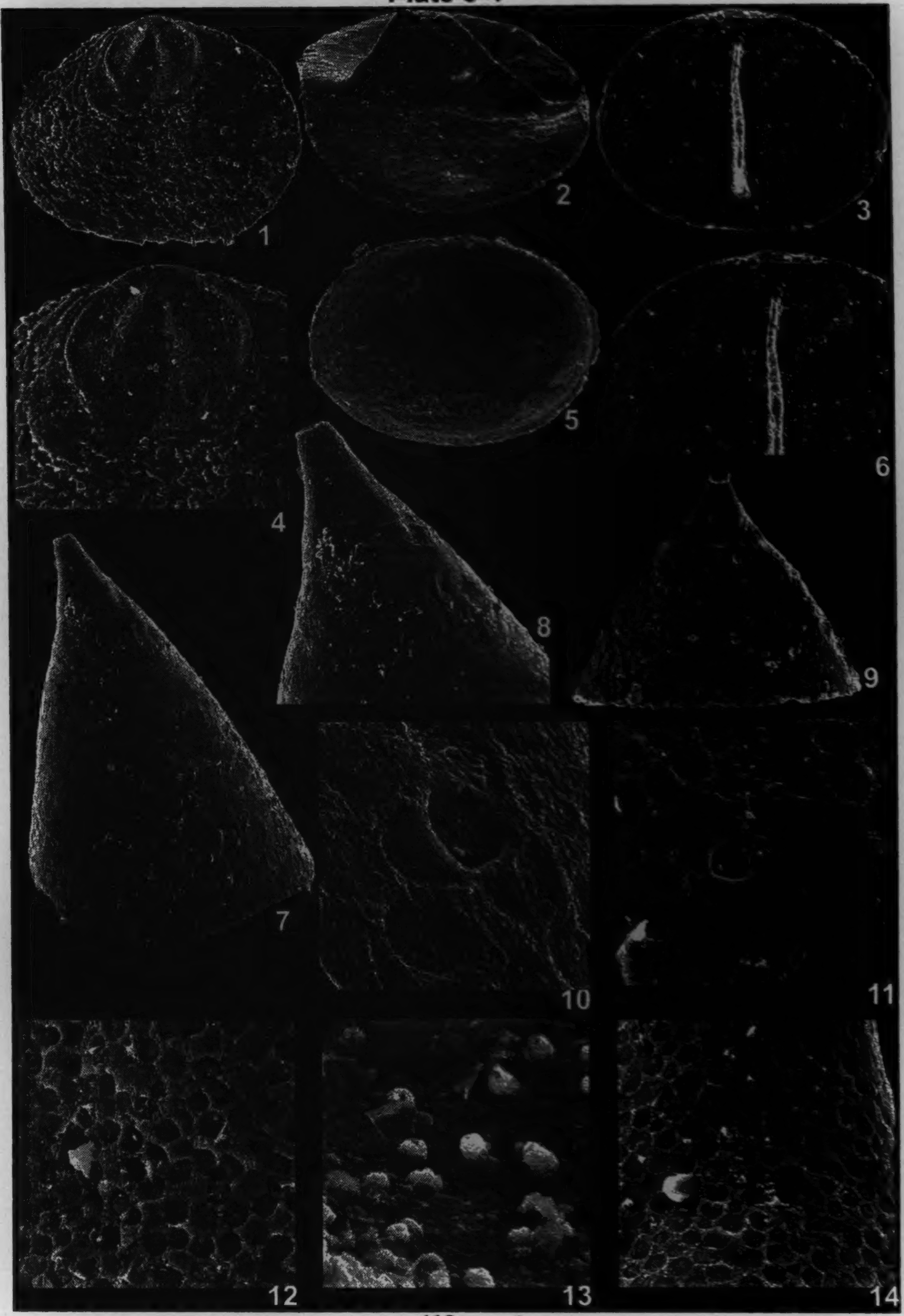
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Plate 3-5 *Opsiconidion emmotus* new species from Wenlock strata, Avalanche Lake in the Mackenzie Mountains, Northwest Territories (AV2 11.5).

2 Lateral view of complete brephic shell; UA 13197; x120.
3 Postero-dorsal view of brephic shell in 1; UA 13197; x120.
4 Internal view of brachial valve; UA 13198; x112.
5 Close up of brachial larval pitting in 1; UA 13197; x1990.
6 Close up of muscle scar of brachial valve in 3; UA 13198; x2306.
7 Close up of posterior part of brachial valve in 3; UA 13198; x189.

Plate 3-5

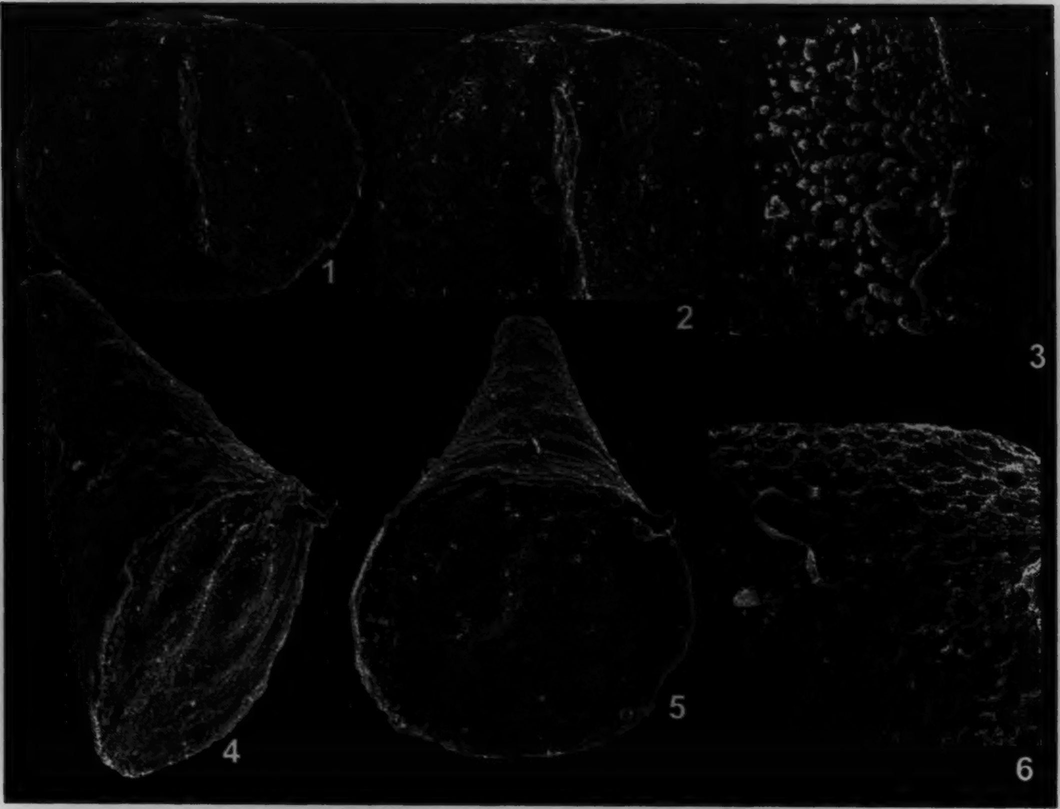

Plate 3-6 *Artiotreta sammera* new species from Wenlock strata of the Cape Phillips Formation, Abbott River, Cornwallis Island (CAR-1).

1. External view of brachial valve; UA 13199; x54.
2. Oblique anterior view of broken pedicle valve; UA 13200; x58.
3. External view of pedicle valve; UA 13201; x100.
4. Internal view of pedicle valve in 3; UA 13201; x75.
5. Internal view of brachial valve in 1; UA 13199; x60.
6. External view of brachial valve; UA 13202; x64
7. Internal view of brachial valve in 6; UA 13202; x72.
8. Oblique lateral view of brachial valve in 7; UA 13202; x72.
9. External view of small brachial valve; UA 13203; x144
10. Internal view of portion of brachial valve in 6; UA 13202; x1400
11. Fragment of pedicle valve; UA 13204; x114.
12. Cross section of pedicle valve in 11 showing thick primary layer and lamellae of secondary layer separated by narrow porous pillar layers; UA 13204; x1040.
13. Section of broken brachial valve showing thick primary layer and lamellae of secondary layer separated by narrow porous layers with pillars; UA 13205; x1600.
14. Close up of brachial larval valve in 6 margin including small portion of adjacent adult shell; UA 13202; x665.
15. Larval pitting from 9 showing minimal cross cutting, and two size sets; UA 13203; x1440.
16. Close up of pitting on the brachial larval valve in 9; UA 13203; x3600.

Plate 3-6

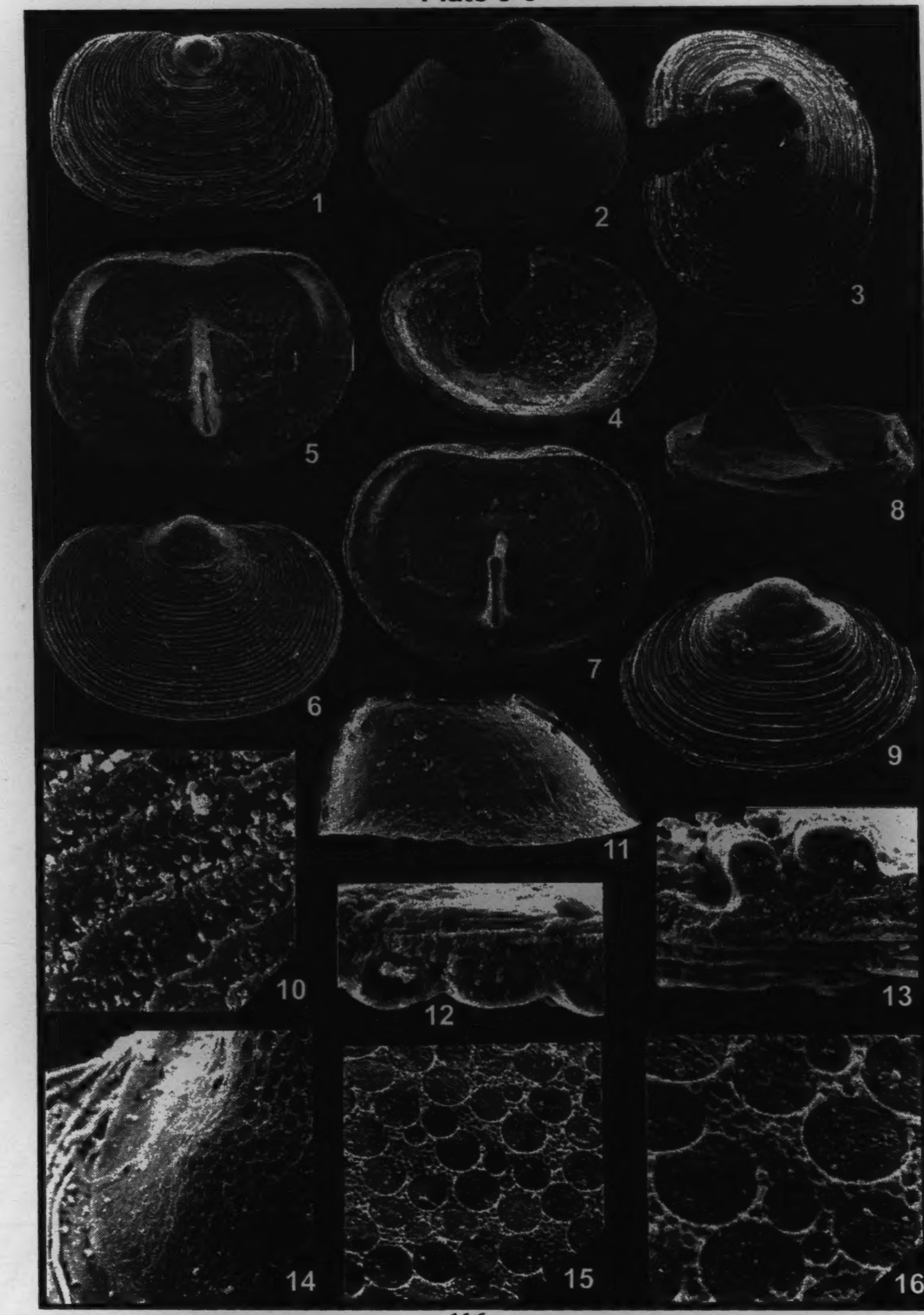
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Plate 3-7 *Artiotreta parva* Ireland from the Wenlock strata of the Clarita Formation, Oklahoma (C1-3).

1. Exterior of brachial valve; UA 13206; x106.
2. Larval valve of 1; UA 13206; x200.
3. Lateral view of brachial valve exterior; UA 13207; x100.
4. Larval valve of 3; UA 13207; x 212.
5. Close up of broken brachial valve in 8; UA 13209; x504.
6. Detail of right muscle scar of 7; UA 13208; x332.
7. Interior of brachial valve; UA 13208; x109.
8. Cross section of broken brachial valve; UA 13209; x222.
9. Oblique lateral view of brachial valve in 7; UA 13208; x98.
10. Ventral view of pedicle valve exterior; UA 13210; x102.
11. Antero-ventral view of pedicle valve exterior; UA 13211; x100.
12. Anterior view of pedicle valve exterior in 10; UA 13210; x99.
13. Dorsal view of pedicle valve interior in 10; UA 13210; x102.
14. Close up of pedicle foramen and muscle scars of 13; UA 13210; x249.
15. Larval valve of 10; UA 13210; x208.

Plate 3-7

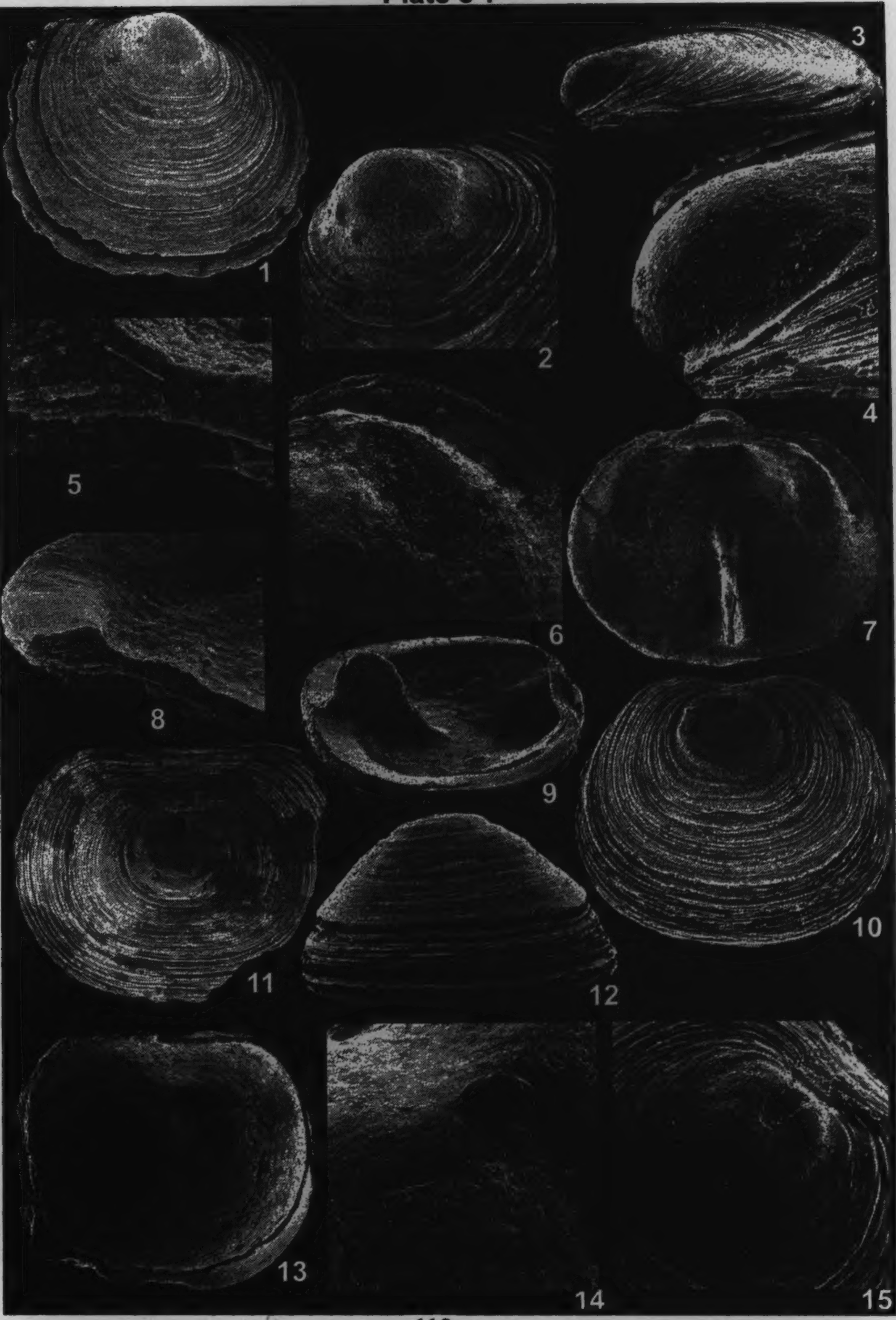
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Plate 3-8 *Artiotreta parva* Ireland from the Wenlock strata of the Clarita Formation, Oklahoma (C1-3).

1. Interior of ephebic brachial valve; UA 13211; x98.
2. Oblique lateral view of brachial valve in 1; UA 13211; x99
3. Interior of brachial valve showing thickening of median septum; UA 13212; x98.
4. Interior of highly advanced brachial valve with thickened septum and shell margins; UA 13213; x97.
5. Oblique lateral view of brachial valve in 4; UA 13213; x97.
6. Oblique lateral view of brachial valve in 3; UA 13212; x98.
7. Larval pitting of pedicle valve; UA 13214; x1541.
8. Dorsal view of small brachial valve; UA 13215; x112.
9. Larval pitting of brachial valve in 8; UA 13215; x 1689.

Plate 3-8

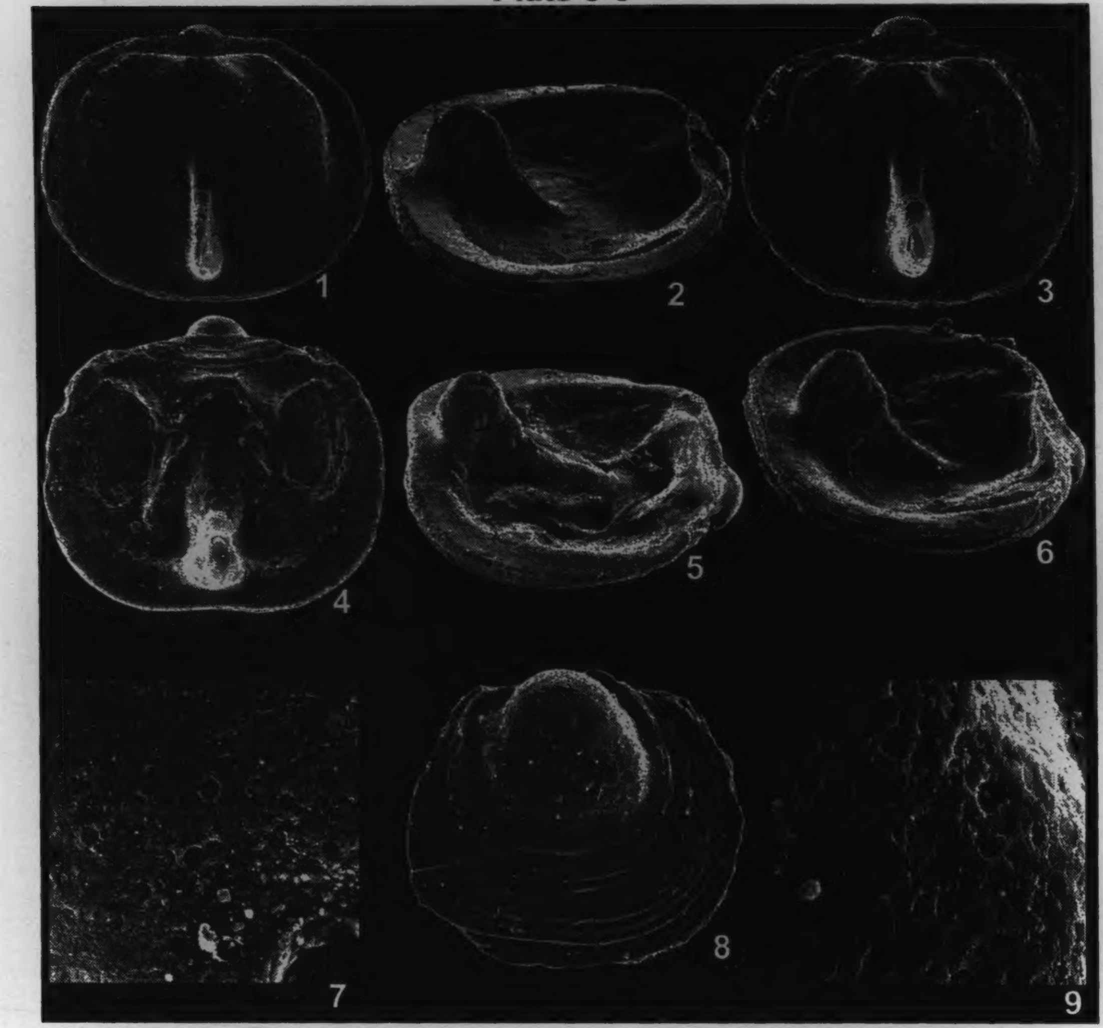
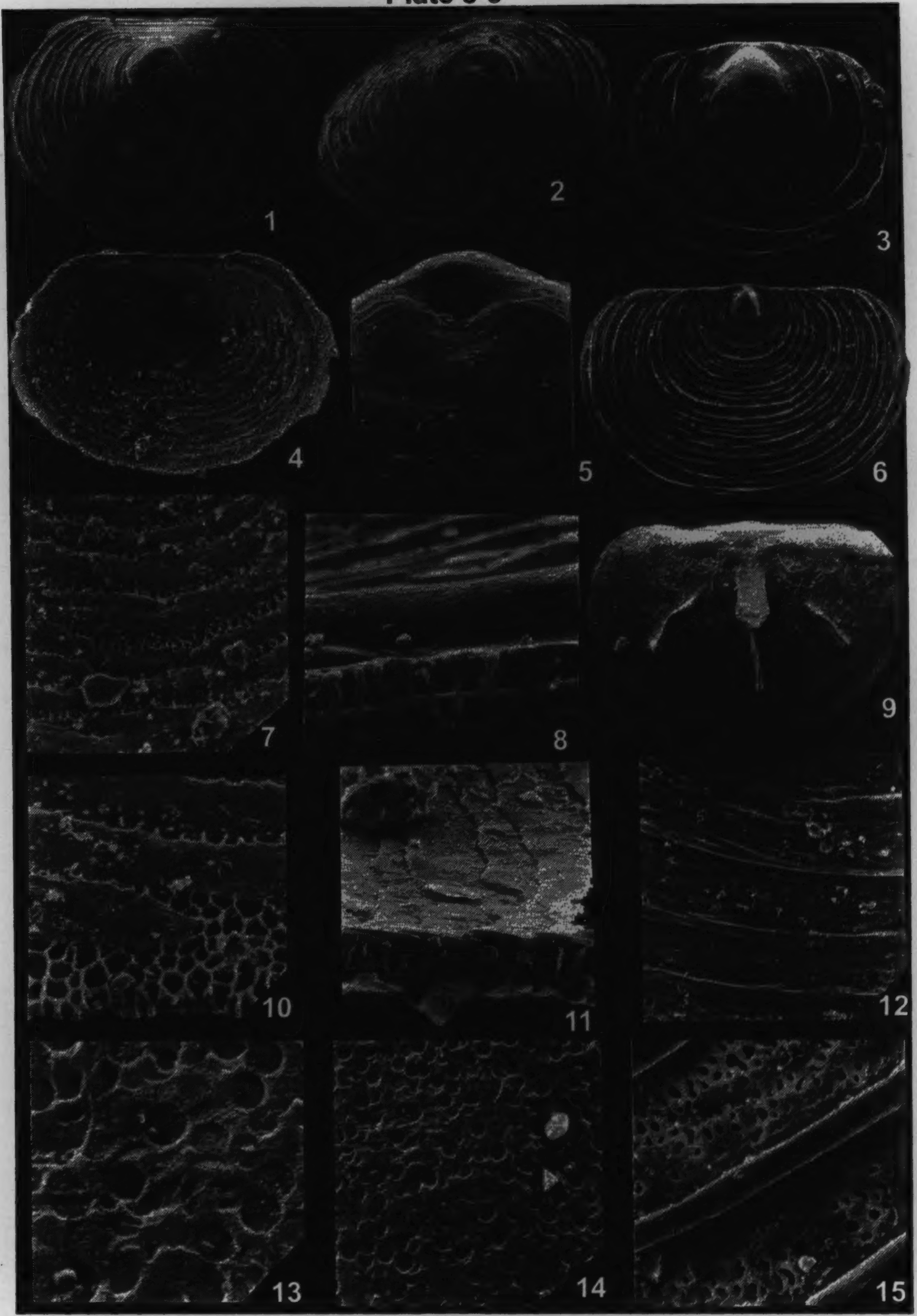


Plate 3-9 *Acrotretella stepplella* new species from Wenlock strata of the Cape Phillips Formation, Abbott River, Cornwallis Island (CAR-1, CAR-80).

1. External view of pedicle valve; UA 13216; x84.
2. Oblique posterior view of 1; UA 13216; x84.
3. External view of broken brachial valve; UA 13217; x120
4. Internal view of 1; UA 13216; x84.
5. Close up anterior view of pedicle foramen of 1; UA 13216; x392.
6. External view of brachial valve; UA 13218; x42
7. Close up internal view of the pedicle valve in 4 showing the inner edges of lamellae and honeycomb pattern of secondary shell; UA 13216; x360.
8. Close up of laminae and pillars of secondary shell layer in broken brachial valve from 3; UA 13217; x1400.
9. Internal view of brachial valve in 6; UA 13218; x43.
10. Internal view of valve margin of pedicle valve in 4 showing honeycombed secondary layer; UA 13216; x720.
11. Close up of broken edge of brachial valve showing pillars and edges of lamellae in 3; UA 13217; x633
12. Close up of external ornamentation of brachial valve in 6 showing distinct fila, faint growth lines, and fine pores; UA 13218; x200.
13. Close up of pitting on the brachial larval valve in 3; UA 13217; x3823.
14. Larval pitting of 3 showing extreme cross cutting of a single size set; UA 13217; x1640.
15. Close up of prosopon ornament showing fila and pores in 6; UA 13218; x782.

Plate 3-9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CHAPTER 4

Using morphology to infer the life mode of highly conical acrotretids.

INTRODUCTION

Acrotretid brachiopods are united by a set of general morphological features that include a minute (1-2 mm), unequally biconvex, laminated organophosphatic shell, a columnar microstructure in the secondary shell layer, a pedicle foramen in the apical region of the pedicle valve, and a small larval shell with a pitted micro-ornament. However, upon a more detailed inspection of the variation within these features, the acrotretids can be informally divided into two morphological groups; one possessing a compact, solidly built shell, well developed pseudointerarea, posteriorly facing pedicle foramen, and discrete larval pits arranged in two size sets, and the other a lightly built, highly conical shell, poorly developed or non-existent pseudointerarea, ventrally facing foramen, and uniformly sized, cross cutting larval pits. It is hypothesized here that this morphological dichotomy is consistent with habitat, as each group's diagnostic characteristics may have provided adaptations to either a benthic or epiplanktonic mode of life. The benthic group is posited to consist of compact, solid forms, which would attach to (or near) the sea floor, while members of the epiplanktonic group are highly conical and may have hung from neuston or other pelagic forms well above the sea floor.

This morphological dichotomy will be delineated through an examination of each group's larval pitting, pedicle foramen direction, conical shape, degree of pseudointerarea development, and shell microstructure. The correlation with habitat can be tested through evidence such as distribution patterns and biofacies associations for each group.

Brachiopod Life Modes

Most brachiopods, both extinct and extant, are thought to have occupied the benthos of the sea, through either an infaunal or epifaunal mode of life. Infaunal forms include the long-lived burrowing lingulids, which have evolved specialized structures such as an extended pedicle and siphons to remain efficient under the sea floor. The rest of the brachiopods are epifaunal living near or upon the sea floor, some attached via a pedicle or encrustation, and others lying loose after pedicle atrophy during ontogeny. Due to their small size, however, acrotretids present something of a problem to workers attempting to infer their life habits. As pointed out by Rowell and Krause (1973) and Cocks (1979), a grain of sand would pose a threat to these minute organisms, so a habitat safe from sedimentation seems the most likely. This habitat may have included areas with weak currents and low sedimentation rain, or ones in which the brachiopods were able to elevate themselves above the sediment surface.

The idea that some small, inarticulated brachiopods were epiplanktonic is not new. Indeed, based on the discovery of these forms in black graptolitic shales, it has been suggested that they may have attached to floating algae, analogous to the fauna inhabiting the seaweed of the Sargasso Sea (Schuchert, 1911; Ruedemann, 1934; Bulman, 1964; Rowell, 1989). These suggestions are equivocal, however, as black shales may also be formed in relatively shallow and oxic environments (Wetzel, 1982). All of this previous work has been based on geological and biological associations, and a strictly morphological approach has not been attempted until now. While this morphological evidence may not be entirely conclusive either, it will lend credence to the idea that at least some of the acrotretids may have invaded the water column, and gained an advantage in doing so.

Valve Orientation

It is important to note that this hypothesis requires a reassessment of the shell orientation in acrotretids (specifically the highly conical forms). The shell of all brachiopods consists of the pedicle valve, which houses all or part of the pedicle foramen, and the brachial valve, which possesses structures for lophophore support. Traditionally, the terms pedicle and brachial are synonymous with ventral and dorsal, respectively, which implies that the pedicle valve, and thus the pedicle are directed ventrally. There are three possible ways the shell of a highly conical acrotretid may have oriented itself about its pedicle (Fig. 4-1). The first two (Figs. 4-1A, 4-1B) retain the traditional orientation with the brachial valve on top of, or dorsal to, the pedicle valve, while in the third orientation (Fig. 4-1A), this relationship is reversed. It seems unlikely that a conical shell made of relatively heavy material such as apatite (specific gravity of 3.1) would float in the water column (Fig. 4-1A), like a balloon anchored by its pedicle. Nor is it parsimonious to suspect that a pedicle passing through such a small foramen would be strong or muscular enough to support and direct such a structure, if it was too heavy to float. Although it is possible that the size of the foramen does not directly control the size of the pedicle (as the pedicle may widen beyond the foramen), it is important to remember that the pedicle will only be as strong as its thinnest or weakest part.

The arrangement pictured in Figure 4-1B requires that the shell lay on the seafloor with its pedicle extended parallel to the substrate, in which case a well-developed pseudointerarea would have been used to stop the cone from rolling around. However, the pseudointerarea in these highly conical forms was usually curved or only slightly flattened and would not have provided any stabilization in such a position. Alternatively, a brachiopod in this position would require a bent, and therefore weakened pedicle, which revisits the problem of strength and efficiency seen in the first arrangement.

The alternative shell orientation (Fig. 4-1C) places the pedicle valve dorsal to the brachial valve in a position suspended from above, like a bell. Given the morphological traits these forms possessed (as will be discussed in further detail below), this seems the most likely orientation of the shell. The pedicle would not need to be overly muscular, as it would serve only as a tether for the suspended shell. In addition, a well-developed pseudointerarea would not be required in such a position, and a completely rounded cone would provide less drag than a flattened edge. It is therefore postulated here that the shells of the 'epiplanktonic' forms would have been oriented with the pedicle valve dorsal to the brachial valve. It follows that the terminology used for each valve should be restricted to 'brachial' and 'pedicle', however, 'dorsal' and 'ventral' can still be used to refer to direction.

Pitting of the Larval Shell

The perimeter of the larval shell in acrotretids is indicated by an interruption in shell growth, as well as a transition in external sculpture from small, round pits to concentric growth lines, marking the shift from a planktonic larva to an attached adult. There are three factors about the pit arrangement and morphology that must be taken into consideration. The first is the number of distinct pit series or sets, as there can be either a single set of uniformly sized pits, or two sets consisting of large series surrounded by pits an order of magnitude smaller. Secondly, the size and morphology of the pits can vary considerably, as there are large (2-6 μm), flat-bottomed and vertical sided pits (essentially shallow cylinders), and/or smaller (0.3-2 μm), concave pits. The third factor involves the degree to which these pits interfere with, or cross cut one another. Although all three of these factors seem to remain constant within acrotretid families (i.e. they have been used as diagnostic characters; Holmer, 1989), it is important to remember that the arrangement of these pits may have more to do with environmental factors than phylogenetic ones, and therefore may be homoplaesous. That is, beyond the specific patterns used for species, general pitting patterns should not be used to characterize high taxonomic levels.

Pit Morphology

The large pits cover most of the larval shell, and appear as circular, flat-bottomed, cylindrical craters in the shell, approximately 1 μm deep (Pl. 4-1, Figs 1-2). The diameter varies considerably (from 2-6 μm) for the whole order, but within families, remains quite uniform, and may be a useful diagnostic character. These pits can exist as discrete, non-cross cutting entities, or they may interfere with one another.

The small pits are generally an order of magnitude smaller than the large pits, with a size range of 0.3-1 μm across (Pl. 4-1, Figs. 3-4). They exist as small, round depressions in the spaces between the larger pits. In taxa where extensive cross cutting is present, these small pits seem to have been obliterated, as the space they occupied is now packed with large, interfering pits only.

The shape and structure of the large pits comply with the cell size for acrotretids and were more likely due to successive resorption by the mantle. Probable cellular structures in acrotretids from the Ordovician are polygonal in shape and average 14-16 µm in diameter (roughly 3 times the size of the large pits).

There are three general pitting types present in the group:

1. Small pits only, with rounded, concave bottoms, up to 2.5µm in diameter; may be surrounded by similar pits an order of magnitude smaller (i.e. 0.8µm in diameter); pits may interfere minimally with one another; present in most Cambrian and Ordovician genera, i.e. *Conotreta* (Fig. 4-2B; Pl. 4-2, Figs. 1-2).
2. Large flat-bottomed pits (up to 6µm in diameter) surrounded by the small concave pits; large pits may interfere with small pits or with one another; present in some Ordovician genera, i.e. *Scaphelasma* or *Artiotreta* (Fig. 4-2C; Pl. 4-2, Figs. 3-4).
3. Large flat-bottomed pits only; up to 6µm in diameter; usually extensive interference; present in Ordovician and Devonian genera, i.e. *Opsiconidion* (Fig. 4-2D; Pl. 4-2, Figs. 5-6).

The pattern and morphology of these larval pits may provide clues to the habitat of some acrotretids. Specifically, the degree to which the large, flat-bottomed pits cross cut one another may indicate how long a larva needed to stay buoyant in the water column before it attached and began its adult life.

The Pit Formation Debate

The formation of these pits has been the topic of much debate, and two major models have been proposed. The Bubble-Raft Model, as first proposed by Biernat and Williams (1970), holds that the acrotretid periostracum had a vesicular nature, containing protein vesicles akin to "bubble rafts formed on the surfaces of liquids by groups of relatively large bubbles which are partially or completely separated from one another by clusters of smaller ones" (p. 496), and that these vesicles left imprints in the underlying shell. Alternatively, Ludvigsen (1974) and von Bitter and Ludvigsen (1979) provided a Selective Resorption Model, suggesting that the mantle interrupted its secretion of the successive shell layers with episodes of selective resorption. More recently, various theories have been advanced in order to dispute the selective resorption hypothesis, alternately citing stacked flattened disk-like vesicles (Williams, 1997), or tablets of silica (Williams *et al.*, 1998) or apatite (Cusack *et al.*, 1999) as responsible for creating these pits. A closer examination and discussion of each of these theories is provided below.

The Bubble Raft

Biernat and Williams (1970) were the first to describe these shallow, flat-bottomed pits in detail, and interpreted them as artifacts of a vesicular periostracum grouped into a coarse set (average 2-4.5 μm in diameter) separated by members of a smaller set (0.35 μm). Through comparison with the periostracum of living Terebratulida, the authors concluded that acrotretid periostraca must have contained small, spherical mucin droplets and large, irregular shaped, protein vesicles (see: Biernat and Williams 1970, text-fig. 1), and that these structures were moulded onto the underlying mineral layer through a thin (10 nm) inner sealing membrane creating the pattern and sets of pits seen on the larval valves. In an extension of their model, this membrane thickens to 0.1µm in the adult acrotretid, which is too thick for the mould to make its imprint on the layer below; thus we do not find these pits on the adult shell. This periostracal bubble raft is proposed to have provided the acrotretid larvae with increased buoyancy. This theory is based on species ranging from Middle Cambrian to Upper Ordovician in age, and especially on the larval valve ultrastructure seen in *Torynelasma*, in which the pits were separate, non cross cutting entities.

Selective Resorption

Ludvigsen (1974) noticed that the pits displayed on the larval valve of a newly described genus, *Opsiconidion*, from the Lower Devonian of Yukon, were closely spaced and cut across one another. He suggested that resorption of the shell was the only mechanism capable of producing the set of cross cutting pits, as the sequence of events would involve successive secretions of thin shell layers interrupted by resorption, by the mantle, of previous shell layers and the pits within (see: von Bitter and Ludvigsen, 1979, text-fig. 3). In recognition of a gradation from the non-overlapping pits described by Biernat and Williams (1970) to the extremely cross cut larval valves in Ludvigsen (1974), von Bitter and Ludvigsen (1979) modified the selective resorption idea, suggesting that the "complexity, degree, and configuration of pitting is dependent on the length of the larval stage" (p. 705). They recognized grades based on the degree of pit cross cutting, wherein increased overlap corresponds with an increased pelagic larval stage. Analogous to the use of frets in airframe or fly reel construction, the resorption pits could have been efficient mechanisms for an acrotretid larva to thicken its shell to maintain strength without adding weight, an important adaptation in the battle to survive in the water column before settling.

Alternative Theories

In recognition of the fact that the bubble raft theory could not completely explain the pitting patterns seen on all acrotretid larval shells (i.e. *Opsiconidion*), Williams worked with various researchers to develop new hypotheses. Williams (1997) noted that the vesicles within the terebratulid periostracum vary from 2 µm spherical bodies to flattened, 250 nm thick disks. Claiming that if the pits were due to selective resorption they should be irregular and have frayed edges (Williams, 1997), he reconstructed the acrotretid periostracum, in which vesicles similar to the flattened disks in terebratulids were stacked against one another in an overlapping arrangement to create the interrupted (or cross cutting) pit pattern (see: Williams, 1997, fig. 227). More recently, Williams *et al.* (1998, 2001) observed that the periostracum of living lingulids includes mineralized structures that may have been responsible for the acrotretid pits. Specifically, the vesicles in the periostracum of discinids contain siliceous tablets that leave imprints in the underlying apatitic shell (Williams *et al.*, 1998; Williams *et al.*, 2001). Similarly, the large, flat-bottomed pits have been attributed to "biconvex tablets of apatite like those exocytosed within the primary layer of the obolid *Linguella*" (Cusack *et al.*, 1999:799).

Discussion

Chia *et al*. (1984) listed a number of density reducing devices utilized by marine invertebrate larvae to counteract a density higher than that of seawater, such as the use of lipids instead of carbohydrates for organic storage, or the development of parachute devices such as setae or spines. Apatite is a relatively heavy biomineral, so these pits may have been the manifestation of such a density reducing device. It is possible that both the bubble raft and selective resorption models were used by various acrotretids, and at various stages in their development. The newly formed larval valve may have reflected a rudimentary vesicular periostracum and was initially covered with the small, round pits that corresponded to small vesicles within the periostracum, as is seen in the pitting type 1 listed above.

The large pits, however, are likely not due to vesicles or bubbles of any kind, as their morphology cannot be reconciled in such a model. If they were artifacts of bubbles, the edges and sides would be rounded. In addition, there is no possible way bubbles could interfere with or cross cut one another, as bubbles in contact tend to form a linear or Y-shaped interface. Therefore, if a suitable settlement site was not available by the time the brachiopod had become too heavy for the effects of the vesicular periostracum, it may have begun resorption of the shell. As proposed by von Bitter and Ludvigsen (1979), this resorption could have proceeded through various stages until an attachment was found. It is conceivable that such a buoyant shell may have been in the water column long and high enough to attach to floating objects. Thus, 'benthic' acrotretids from the Ordovician should possess both sets of pits, as they may have begun resorption to prolong the larval stage in wait for a suitable settlement site. While those with large, uniformly sized, cross cutting pits, which are generally younger (Ordovician-Devonian), may have been 'epiplanktonic', having capitalized on the advantage of increased buoyancy and invaded the waters above the sea floor.

Additionally, the pitting patterns listed above may follow an evolutionary template. In acrotretid species from the Cambrian, and some from the Ordovician (as described in pit arrangement 1), only small-scale, rounded pits are present, indicating that the vesicles of the periostracum may have provided the sole means for buoyancy. Throughout the Ordovician and into the Devonian, however, the large, flat-bottomed pits begin to appear in certain genera (i.e. *Scaphelasma* and *Opsiconidion*) and the degree of cross cutting increases.

Arguments to the contrary (i.e. Biernat and Williams, 1970; Williams *et al*., 1998; Cusack *et al*., 1999; Williams *et al*., 2001) seem only to cloud the problem by using unrealistic models and homologies. For example, it is tenuous to assume that an acrotretid periostracum would be similar to that of a terebratulid (Biernat and Williams, 1970; Williams, 1997), given that the two groups are in different subphyla. In fact, the periostracum of terebratulids (see: Williams, 1997, fig. 227-1) looks nothing like that of the reconstructed acrotretid periostracum (see: Biernat and Williams, 1970, text-fig. 1; and Williams, 1997, fig. 227-3, 227-5).

Similarly, the idea that the large pits are moulds of siliceous and/or apatitic tablets (Williams *et al*., 1998; Cusack *et al*., 1999) is unlikely. Although the homology is drawn from linguliformean taxa more closely related to acrotretids than terebratulids, it remains a theory irreconcilable within the morphology of the pits themselves. In the lingulid genus *Wahwahlingula* from the Cambrian-Ordovician boundary in Utah (Popov *et al*., 2002), both larval and post-larval pits are present (Pl. 4-1, Figs 5-8). Those of the larval shell differ from acrotretid pits in arrangement, size, and shape. They are packed neatly in rows, never cross cut, are up to 1 μm in length, and are subrectangular in outline. The post larval pits have a more rounded outline and bottom than the larval pits, but are a similar size. Both the larval and post larval pits are similar to those left by the biconvex tablets of apatite described by Cusack *et al.* (1999) in *Linguella*, and it is likely that these types of pits are artifacts of such features.

In summary, it is most likely that vesicles or mineralized, biconvex tablets would create a round-bottomed impression in the underlying shell, as is seen in the recently described linguliformeans from Utah (Popov *et al.* 2002), and in the Cambro-Ordovician pitting arrangement 1 in the acrotretids. However, while these various hypotheses put forth by Williams and his group may be useful in the explanation of the small round pits, the large, flat-bottomed pits (which are the most important in this study on a possible epiplanktonic habitat in the acrotretids) remain irreconcilable within each theory, leaving the idea of selective resorption (Ludvigsen, 1974; von Biter and Ludvigsen, 1979) as the most plausible and parsimonious interpretation.

Features of the Adult Shell

These series of selective resorption events could have afforded the larva a prolonged stage of buoyancy, allowing it to reach substantial heights in the water column. In order for the brachiopod to remain there, however, the adult shell must have evolved adaptations to the change in life mode. These adaptations included a highly conical shell with no pseudointerarea and an apically directed foramen.

Conical Shape

Acrotretid brachiopods possess a conical pedicle valve. The cone varies in height, however, from low and rounded, to high and peaked. Those forms with a low, rounded profile (Pl. 4-3, Fig. 6) are posited to have lived attached near the sea floor, while the highly conical forms (Pl. 4-3, Fig. 1) possessed a shape ideal for hanging. They would have been oriented with the peak of the pedicle valve closest to their attachment site, and therefore, the brachial valve could open into the water column.

Pseudointerarea

The pseudointerarea is a flattened area at the back of the brachiopod shell. In the pedicle valve, it consists of two flat plates on either side of a raised inter-ridge or a depressed intertrough. The 'benthic' forms have a very well developed pseudointerarea (Pl. 4-3, Fig. 6), giving the shell a D-shape at the commissure. They may have used this flattened area to rest their shell on the substrate in order to keep their gape oriented into the direction of flow. The pseudointerarea of the 'epiplanktonic' forms, on the other hand, is relatively non-existent (Pl. 4-3, Fig. 1), as the back of the shell is curved or only slightly flattened. If these forms are indeed hanging high in the water column, the advantage conferred by a flattened posterior shelf is absent.

Pedicle Foramen

The pedicle foramen in acrotretids is a small, circular opening at the apex of the pedicle valve that provides an exit for the fleshy pedicle. The larval shell possesses a fully enclosed foramen in all acrotretid families except for some scaphelasmatids, where it is only partially enclosed. In the hypothesized benthic forms, this foramen is directed posteriorly (Pl. 4-3, Figs. 6-7) and would have guided the pedicle towards an attachment site below and behind the brachiopod. In those posited to be epiplanktonic, however, the foramen is located at the valve apex and is directed apically (Pl. 4-3, Figs. 2-3). If these forms were, as proposed, hanging from other objects, whether in the plankton or near the sea floor, the pedicle would have been extended upward relative to a vertically oriented pedicle valve. The brachial valve would have formed a small cup at the base of this dangling elongate conical structure.

Additionally, the position of the foramen relative to the pseudointerarea is of interest here. In the 'benthic' forms, the pedicle foramen opens perpendicular to the pseudointerarea, so if the shell was resting on that flat surface, a short pedicle could have attached to the surface without bending. In the 'epiplanktonic' forms, the foramen opens in a direction parallel to the 'pseudointerarea' or posterior side of the shell, which would have produced a straight pedicle if the long axis of the shell was vertical, but turned through a right angle if the shell was lying on its side.

Shell Structure

The shell in all acrotretids is comprised of two mineralized layers, overlain by an organic periostracum. The primary layer is that which is laid down first and is invariably solid. The secondary layer is quite variable within the Acrotretida, but is generally comprised of layers of vertical rods separated by empty spaces in between solid horizontal lamellae. The rods are sometimes modified into a polygonal network of walls giving a honeycomb pattern to the secondary layer. Holmer (1989) also identified a tertiary layer in the Acrotretidae and Torynelasmatidae that consists of laminae similar to columns and lamellae in the secondary layer. However, it is difficult to discriminate between the tertiary and secondary layers, so this distinction may be artificial. Although the relatively empty secondary layer occurs in all acrotretids, and is indeed a synapomorphy for the group, the degree of total shell porosity varies considerably among acrotretids and is used here to delineate the two proposed groups.

Shell Structure of the 'Benthic' Group

In the genus *Artiotreta*, the primary layer is a solid structure composed of sheets of granular apatite laid upon one another (Pl. 4-3, Figs. 8-9). The secondary layer is camerate (as proposed for the Scaphelasmatidae; Holmer, 1989), which consists of lamellae connected by solid perpendicular walls. There are only a few laminae within the secondary layer, giving the shell a heavy and compact quality.

Shell Structure of the Epiplanktonic Group

In contrast to the dense nature of the shell in *Artiotreta*, genera such as *Opsiconidion* and *Biernatia* possess many laminae of camerate and columnar layers in their secondary shell, making their shells lighter overall. It is possible that the porous nature of even the 'benthic' acrotretids may have served as an exadaptation for these highly conical forms, thus conferring an advantage in the pursuit of an epiplanktonic existence. Indeed some of the Cambrian and Ordovician acrotretids with shell morphologies of the 'benthic' type have quite porous regions of secondary shell, especially where secondary thickening has taken place.

The Epiplanktonic Acrotretid

Members of the family Biernatidae provide the best example of what may have been an epiplanktonic acrotretid. They are all highly conical forms, generally with large, extensively cross cutting pits in the larval shell, apically directed foramina, and highly porous secondary layers. *Opsiconidion* is a long-lived and broadly distributed genus within the family, as it extends from the Early Ordovician of Wales to the Early-Middle Devonian of northern Canada, Russia and Australia. Indeed there are at least four species known from the Emsian (Fig. 4-3). Additionally there is an undescribed *Opsiconidion* species from the Upper Devonian of New York (R. Huson, pers comm.). While there is much variation in features such as cross cutting and foramen direction within the genus, perhaps this distribution and range can be attributed to the invasion of a novel life mode. A life mode safe from sediment rain, high up in the water column, made possible by morphological adaptations such as a lightly built, highly conical shell with no flattened edges and an apical, ventrally directed foramen, with a long live planktonic larval stage to get the animal up there. The species *Opsiconidion arcticon* Ludvigsen represents the pinnacle of this morphology.

Although analogies of this 'escape the bottom' strategy do not abound, there are a few examples in the invertebrate world that may provide some parallels. Crinoids of the family Scyphocrinitidae from the Siluro-Devonian of Morocco are thought to have lived in a planktonic habitat (Hess, 1999). Crinoids are generally thought to be benthic animals, attached by means of a holdfast and cirri. The scyphocrinitids are thought to have moved from a benthic habitat to a planktonic one, through the transformation of their cirri into chambered bulbs called loboliths (Haude, 1972). These loboliths are thought to have functioned as buoys (Schuchert, 1904; Bather, 1907), thus suspending the stem and calyx of these crinoids just below the water surface (Haude *et al.* 1994). This invasion of a niche previously unoccupied by crinoids would likely have given the scyphocrinitids an advantage. Similarly, the pentacrinitid, *Seirocrinus* is interpreted to have possessed a pseudoplanktonic life mode, in which the holdfast had been modified for attachment to floating logs (Haude, 1979).

The so-called 'bubble raft snail', *Janthina*, provides the best example of the adaptation of a traditionally benthic organism to a life in the plankton. *Janthina* blows a bubble raft that sits just above the surface of the water. The animal itself, inside a lightly built shell, hangs upside down from the bubble raft and uses it to propel through the water. Additionally, the bubble raft houses the developing larvae, which upon hatching "enjoy a brief life of 'free flight' before their shells become too heavy and bubble rafts must be constructed to replace ciliary action by buoyancy" (Parks, 1976: 75).

Summary

Brachiopods are generally thought to be benthic, sedentary filter feeders. For most of the Rhynchonelliformeans, this habitat was suitable enough for a few genera to survive until today. For the linguliformeans, however, intensive competition with their larger, articulated cousins as well as with the radiating bivalve molluscs in the Ordovician, may be the reason why only those with non-traditional habitats (such as the burrowing *Lingula)* thrived. One such non-traditional habitat, the invasion of the plankton, may have evolved in the acrotretids, and allowed the group to survive in to the

Devonian. Equally novel 'escape from the bottom' strategies occur with the scyphocrinitid and pentacrinitid crinoids, as well as the bubble raft snail, *Janthina*.

As has been shown, selective resorption (creating the large flat-bottomed pits) likely occurred in non-epiplanktonic forms, such as *Scaphelasma* and *Artiotreta*. For these genera, a lighter larva would likely have been able to find a better settlement site. For those posited to be epiplanktonic, the resorption was extreme and created a light larva capable of reaching and attaching at great heights in the water column. The evolution of an adult morphology adapted for this hanging mode of life (with a highly conical shell, an apically directed foramen, and no pseudointerarea), served to keep the brachiopod there after settlement. There they thrived, and were the last remaining members of a group that evolved in the Cambrian and were dominant throughout the Ordovician.

Figure 4-1

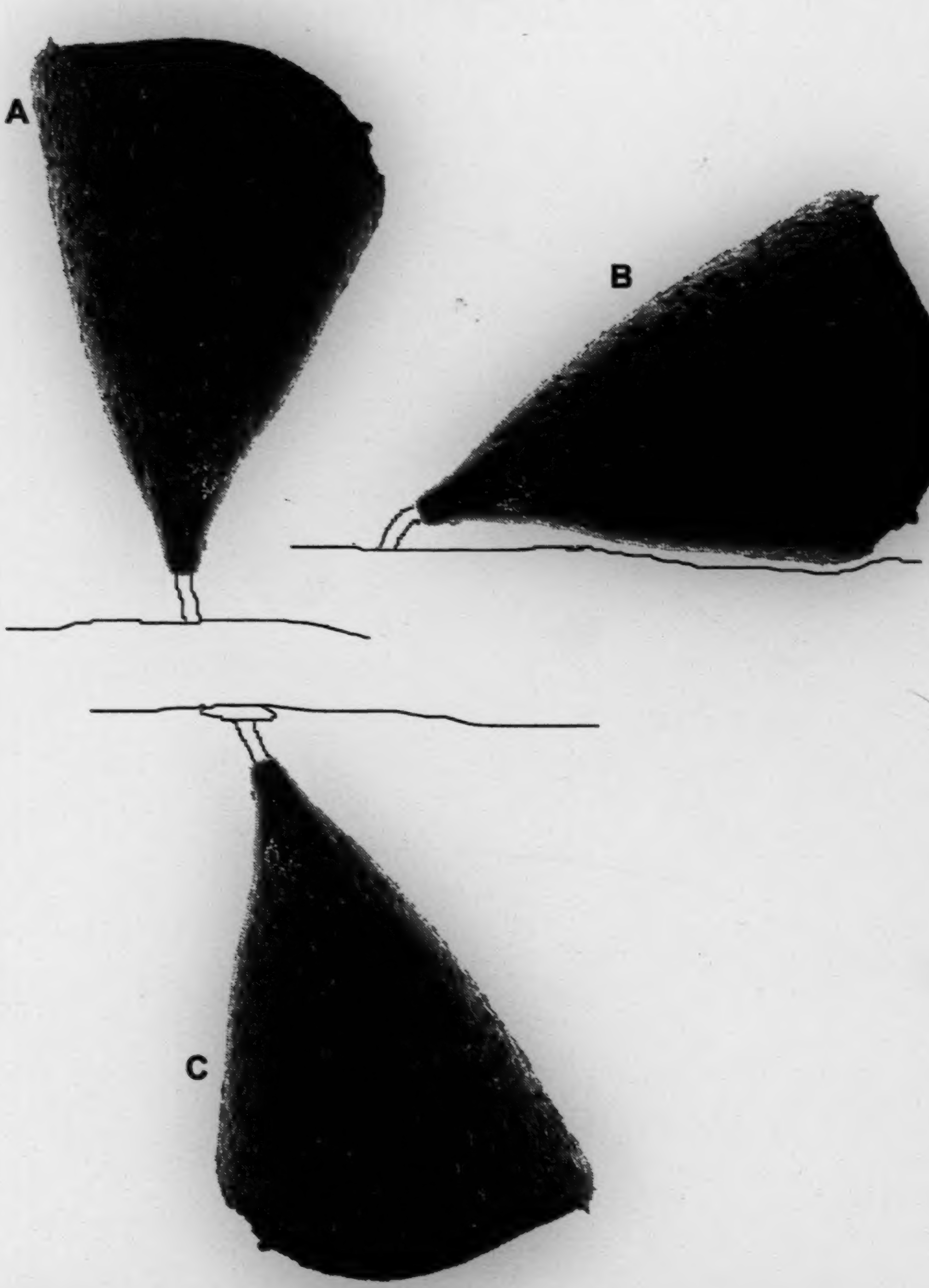


Figure 4-1: Three alternative orientations to the pedicle valve in a highly conical acrotretid, *Opsiconidion emmottus*. C seems the most parsimonious.

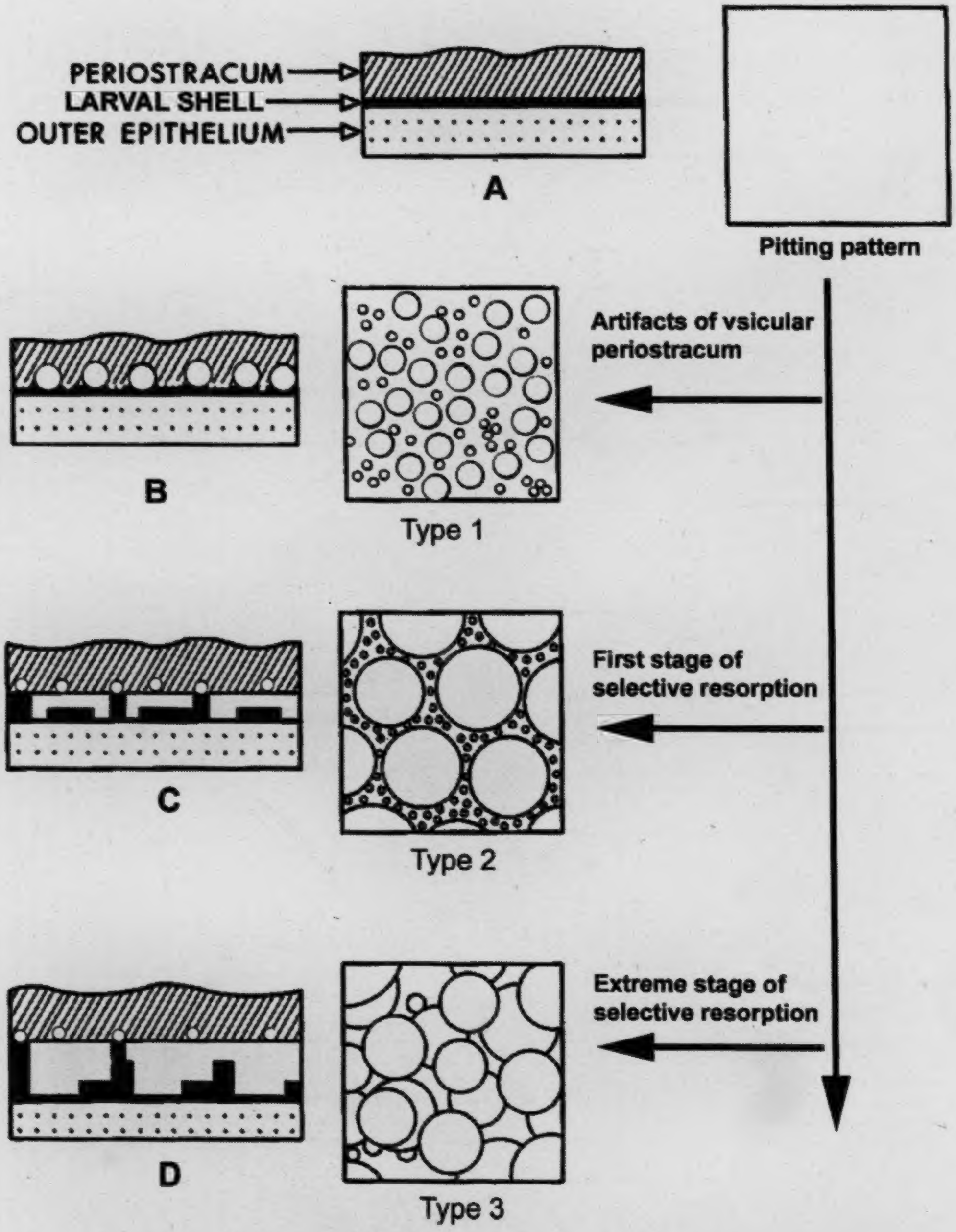

PERIOSTRACUM
LARVAL SHELL
OUTER EPITHELIUM
A
Pitting pattern
Artifacts of vsicular periostracum
B
Type 1
First stage of selective resorption
C
Type 2
Extreme stage of selective resorption
D
Type 3

Figure 4-2: Alternative to von Bitter and Lugvigsen (1979) sequence of of events, combining the Buble Raft Theory (Biernat and Williams,1970) and Selective Resorption. It is hypothesized here that all acrotretids go through stage A-B, but that resorption (C) only occurs in a few genera, and procedes to extremes (D) in OPSICONIDION only.

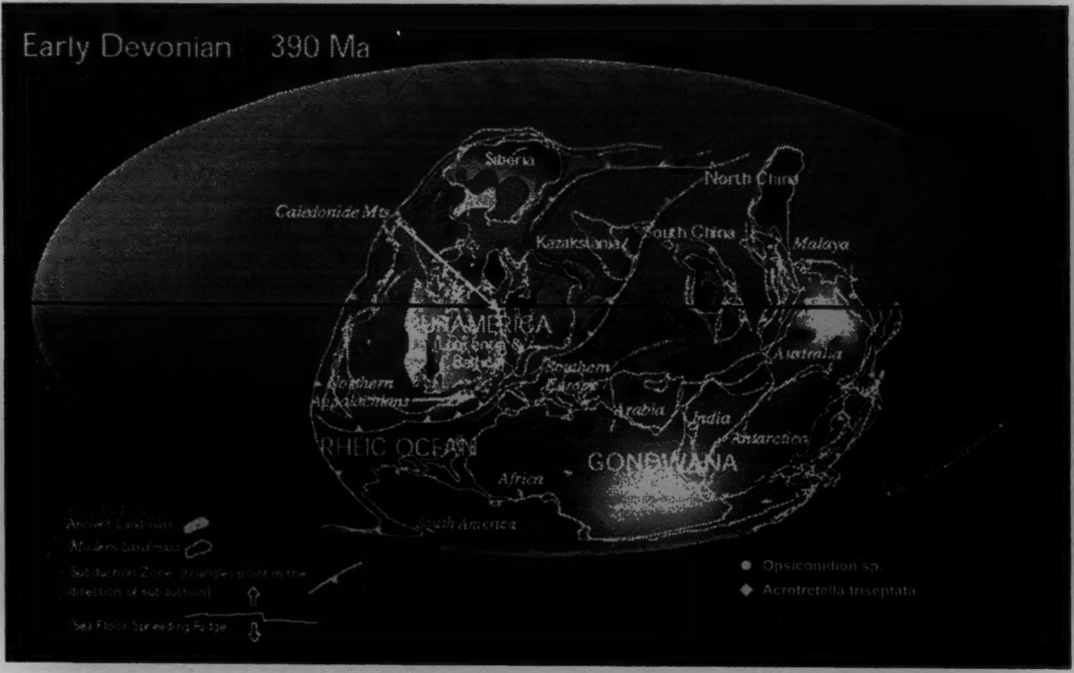

Early Devonian 390 Ma
Siberia
North China
Caledonide Mts
Kazakstania
South China
Malaya
EURAMERICA
Laurentia & Baltica
Southern Europe
Northern Appalachians
Australia
Arabia
India
Antarctica
RHEIC OCEAN
GONDWANA
Africa
South America
Ancient Landmass
Modern Landmass
Subduction Zone (triangles point in the direction of subduction)
Sea Floor Spreading Ridge
● Opsiconidion sp.
◆ Acrotretella triseptata

Figure 4-3: Distribution of acrotretids in the Early Devonian. Numbers refer to the number of species present. (modified from Scotese, 2000)

Plate 4-1 Comparison of the pit types.

1-2 *Opsiconidion emmotta*, from the Lower Silurian of the Northwest Territories; two views of the large flat-bottomed pits showing a cross cutting relationship; Fig. 1 x4000, Fig. 2 x2000.

3. *Hisingerella gualcamayensis*, from the Lower Ordovician of Argentina; showing the small, concave pits; Fig. 3 x2200.

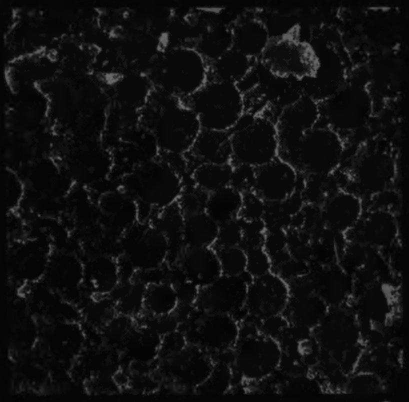
4. *Tasbulakia ondata*, from the middle Ordovician of Argentina; close up of single small pit; x20000.

5-8 *Wahwahlingula*, from the Cambro-Ordovician of Utah; Fig. 5 brachial valve,x39 (Popov *et al.*, 2002, fig. 5-19), Fig. 6 close up of larval pitting, x1500 (Popov *et al.*, 2002, fig. 5-4), Fig. 7 pitting on the adult shell x560 (Popov *et al.*, 2002, fig. 5-11), Fig. 8 close up of pitting on the adult shell, x1800 (Popov *et al.*, 2002, fig. 5-12).

Plate 4-1

1

2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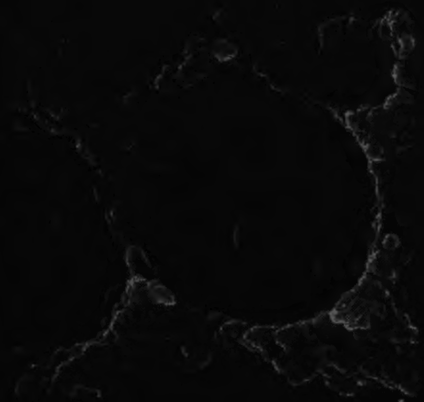
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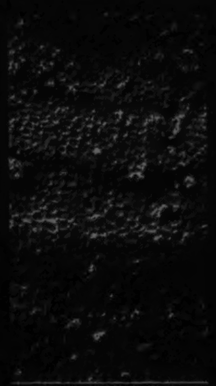
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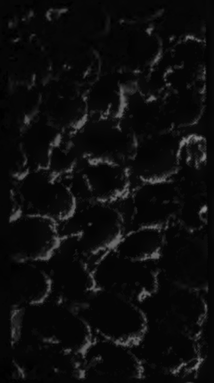

8

Plate 4-2 Pitting Types

1-2 Pitting Type 1 : small pits only. *Hisingerella gualcamayensis* from the Lower Ordovician of Argentina; Fig. 1 x50, Fig. 2 x2000.

3-4 Pitting Type 2: large pits surrounded by small ones. *Scaphelasma naithum* from the Lower-Middle Ordovician of Argentina; Fig. 3 x60, Fig. 4 x1600.

5-6 Pitting Type 3: large pits only, extensive cross cutting. *Opsiconidion arcticon* from the Lower Devonian of the Northwest Territories; Fig. 5 x35, Fig, 6 x2100.

Plate 4-2

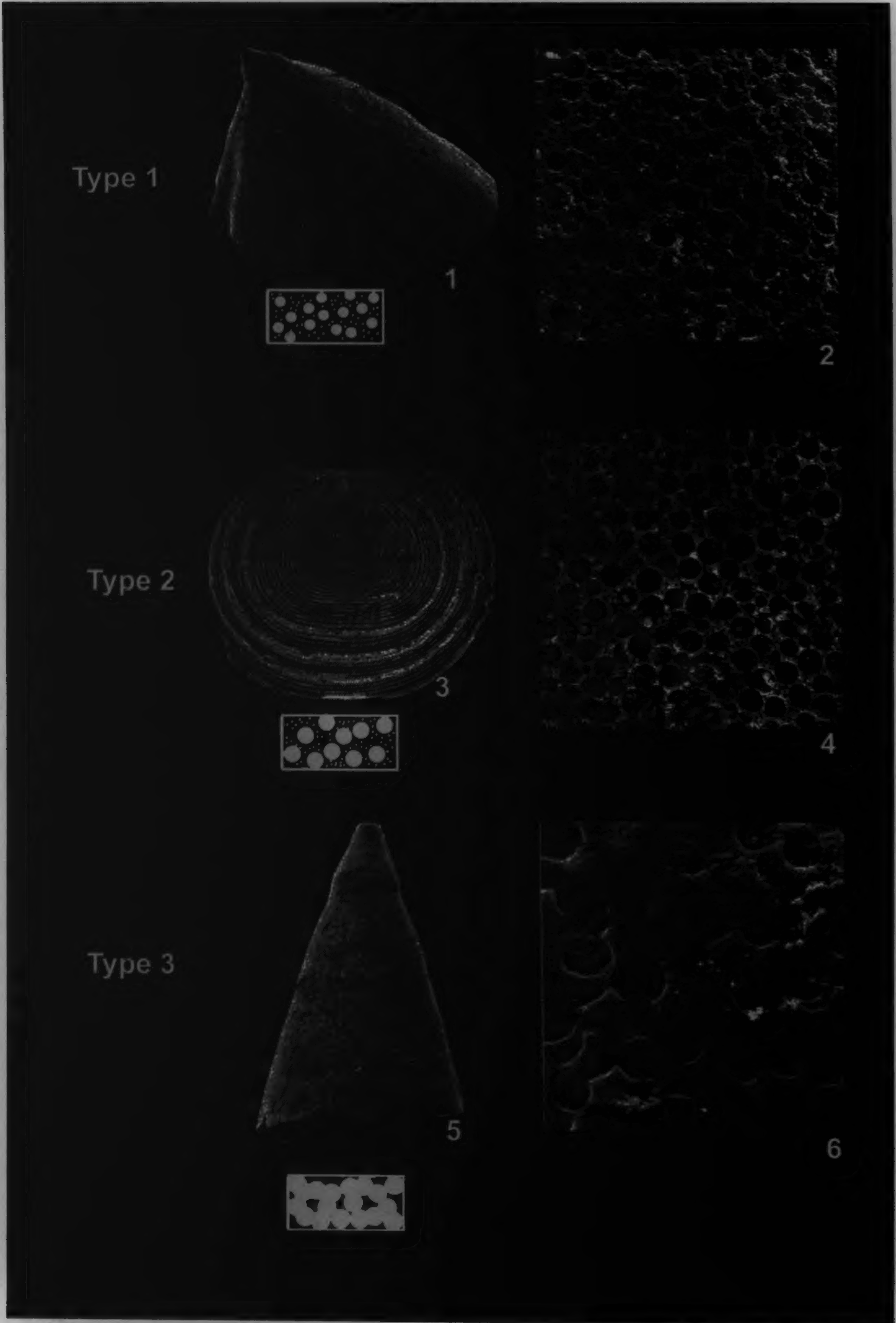
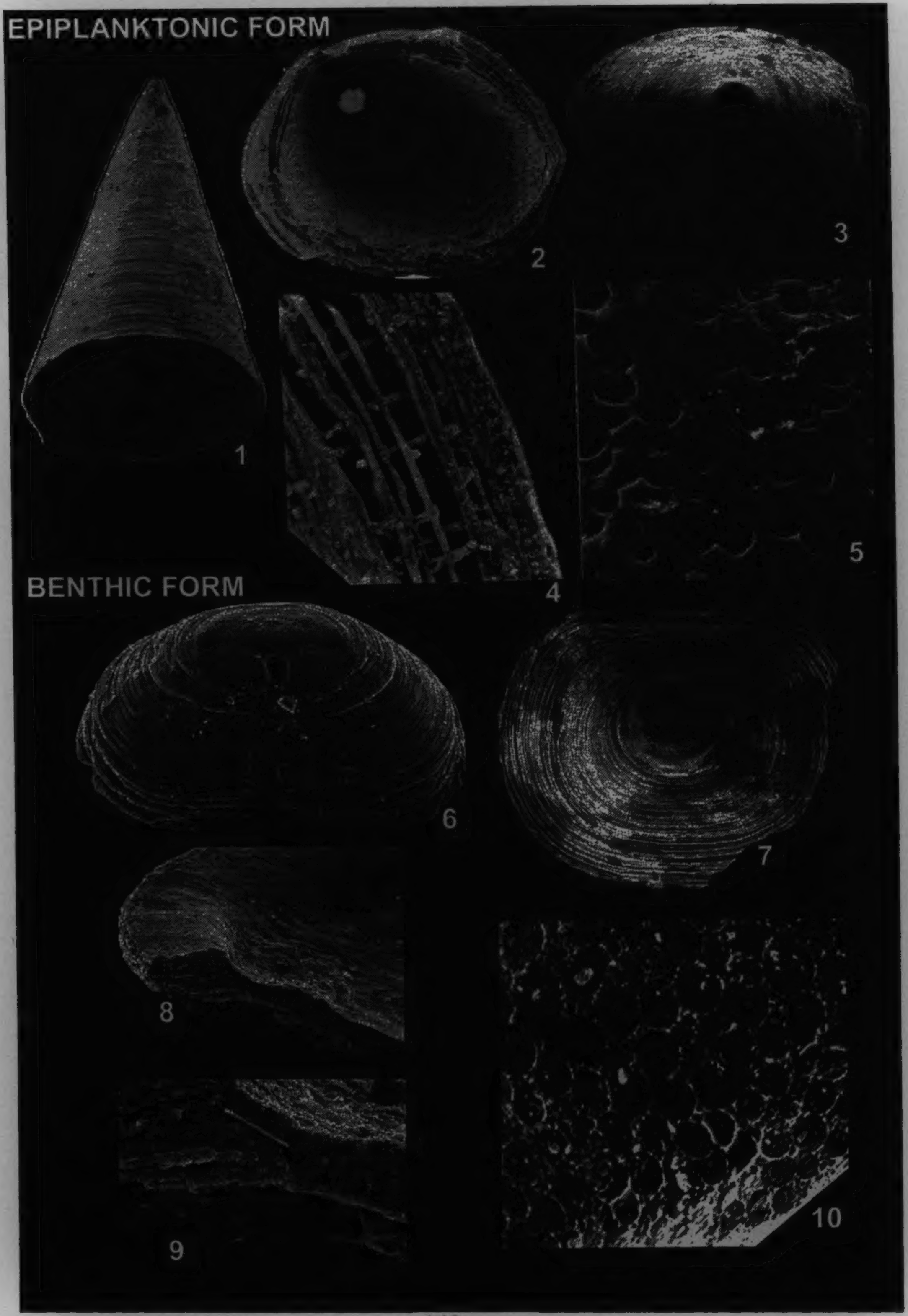

Type 1
1
2
Type 2
3
4
Type 3
5
6

Plate 4-3 Comparison of Epiplanktonic and Benthic forms

1-5 Epiplanktonic form-*Opsiconidion arcticon* Ludvigsen, from the Lower Devonian of the Northwest Territories; Fig. 1 x80, Fig. 2 x85, Fig. 3 x80, Fig. 3 x1200, Fig. 4 x2100.

6-10 Benthic form-*Artiotreta parva* Ireland, from the Middle Silurian of Oklahoma; Fig. 7 x160, Fig. 7 x140, Fig. 8 x200, Fig. 9 x250, Fig. 10 x2300.

Plate 4-3


EPIPLANKTONIC FORM
1
2
3
4
5
BENTHIC FORM
6
7
8
9
10

CHAPTER 5

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